

## Catalogue of American Amphibians and Reptiles.

Heyer, W.R., M.M. Heyer, and R.O. de Sá. 2010.  
*Leptodactylus savagei*.

***Leptodactylus savagei* Heyer**  
**Savage's Thin-toed Frog**

*Cystignathus pentadactylus*: Cope 1887:18.

*Leptodactylus pentadactylus*: Noble 1918:323.

*Leptodactylus pentadactylus dengleri*: Taylor 1952:  
649.

*Leptodactylus pentadactylus pentadactylus*: Gans  
1958:1.

*Leptodactylus dengleri*: Goin 1959:136.

*Leptodactylus pendactylus*: Savage and Villa R.  
1986:23. *Lapsus*.

*Leptodactylus pentadactylus*: Savage and Villa R.  
1986:104. *Lapsus*.

*Leptodactylus savagei* Heyer 2005:330. Type-locality, "Rincon de Osa, Puntarenas, Costa Rica, 08° 42'N, 83°29'W." Holotype, National Museum of Natural History, Smithsonian Institution (USNM) 227652, adult male, collected by Miriam H. Heyer and W. Ronald Heyer on 11 June 1973.

• **CONTENT.** The species is monotypic.

• **DEFINITION.** Adult *Leptodactylus savagei* are large, the head is as wide as long or usually wider than long, and the hind limbs are moderate in length (Table 1; Heyer and Thompson (2000) provided definitions of adult size and leg length categories for *Leptodactylus*). Male vocal sacs are not visible externally. Sexually active males have hypertrophied forearms, usually 1 large black spine on each thumb, rarely with 1 large spine and a prepollical bump, and a pair of black chest spines. A pair of entire dorsolateral folds extend anteriorly from at least one-half to full distance from eye to groin, the dorsolateral folds are rarely interrupted. Flank folds (diverging from the supratympanic fold at the uppermost posterior portion of the tympanum and extending as far as the lower flank at mid-body level) range from entire (often) to only a dark spot/wart (rarely) in the area where the fold would be between the tympanum and shoulder. Lateral folds are not distinguishable. The toe tips are

**TABLE 1.** Summary measurement data for *Leptodactylus savagei* (means are in parentheses).

Measurement	Males	Females
SVL (mm)	106–156 (133.2)	110–164 (137.1)
Head length/SVL (%)	33–40 (38)	34–40 (37)
Head width/SVL (%)	36–44 (39)	33–42 (38)
Thigh length/SVL (%)	37–47 (42)	37–46 (42)
Shank length/SVL (%)	40–49 (44)	39–48 (44)
Foot length/SVL (%)	38–51 (46)	40–51 (46)

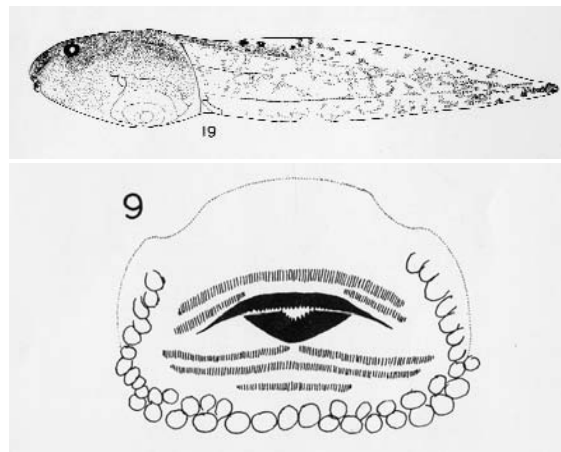
rounded and either barely wider than or of equal width as the toes immediately behind the tips. The toes have weak to noticeable lateral ridges and either



**FIGURE 1.** *Leptodactylus savagei*, Rincon de Osa, Puntarenas, Costa Rica. Photograph by Roy W. McDiarmid.

lack any web or (usually) have vestigial webbing between toes I-II-III or I-II-III-IV. Metamorphic and slightly larger juveniles lack webbing and either have very weak lateral ridges or lack them. The upper shank surfaces almost always have some texture, including a shagreen and/or small black or white tubercles. The outer surface of the tarsus may either be smooth or with a shagreen or small black or white tubercles. The sole of the foot is typically smooth, lacking texture.

The upper lip lacks a distinct light stripe and usually has dark triangular marks, 1 or 2 of them elongate and approaching or entering the lower eye; the upper lip is rarely uniformly light. The dorsal pattern is quite variable, usually with irregular quadrangular or rectangular markings of equal or alternating lighter/darker intensity, confluent laterally or not, or the dorsum often is uniform light or dark, or uniform light with one or two well-defined narrow transverse dark bands, or the dorsum rarely has more than two dark transverse bands of equal intensity in addition to an interorbital band, sometimes with the transverse bands confluent laterally. The supratympanic fold is dark brown. The dorsolateral folds are outlined with dark brown. There are no middorsal stripes. The belly is dark with large or small light vermiculations, or dark with small or large discrete light spots. The pattern of the posterior



**FIGURE 2.** Tadpole of *Leptodactylus savagei*, figures 9 and 19 in Heyer (1970 [1968]), based on a specimen from Costa Rica. Tadpole length 41.3 mm, width of oral disk 2.7 mm. Tail myotomes not illustrated.

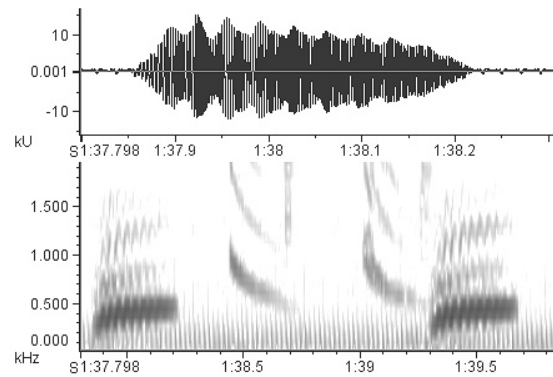
surface of the thigh is variable, including dark with small to large distinct light vermiculations (vermiculations sometimes coalesced in part), or a dark back ground with contrasting large and light irregular blotches/spots extending from light dorsal transverse bars. The rest of the thigh is dark with light vermiculations, or rarely labyrinthine, or rarely mostly distinctly light with a few irregular dark marks.

Juveniles are often mistaken as a different species by individuals in the field for their first time, as the mid-dorsal areas are much more red/brown than adults (J.M. Savage pers. comm.; Heyer 2005:283).

The facultatively carnivorous larvae are elongate and have characteristics of both the lentic exotrophic, carnivorous and lentic suspension feeder guilds (McDiarmid and Altig 1999, guilds 5 and 7). The oral disk is positioned almost completely anteriorly and entire (not emarginate). There is a single row of marginal papillae laterally, a broad rostral gap lacking papillae, and various combinations of a single and/or double row posteriorly. There are no submarginal papillae. The tooth row formula is 2(2)/3(1). The interrupted A-2 row consists of two short rows of teeth. Row P-3 is about half the length of row P-2. The spiracle is sinistral and the vent tube is median. The dorsal fin originates at the tail/body juncture or at the first or second tail myotome. The lateral line system is visible under magnification on the dorsal and lateral head-body region. Larval total length at Gosner stages 29–30 ranges from 32.2–34.8 mm; stages 34–36 range from 53.6–63.8 mm. Body length of stage 29–30 larvae ranges from 9.0–9.8 mm, stage 34–36 from 13.0–14.1 mm. Eye diameter is 10–11% of body length. The width of the oral disk is 17–20% of body length. The dorsum is tan to brown with denser concentrations of melanophores posteromedially to the nostrils and on either side of the tail musculature on the body. The oral disk is suffused with melanophores or not; if melanophores are present, they extend posteriorly to the midventer. The anal tube has few or no melanophores. The tail fins and musculature are blotched.

The advertisement call consists of a single note per call, given at rates of 40–49 calls/min. Call duration ranges from 0.24–0.42 s. Calls have 5–13 pulses/call, with a mean pulse rate among individuals of 31–46 pulses/s. The call is intensity modulated, starting and ending quietly. The call is frequency modulated, a rising whoop, with a mean initial frequency among individuals of about 300–345 Hz. The mean dominant frequency among individuals ranges from 350–520 Hz. The call has harmonic structure (Figure 3).

• **DIAGNOSIS.** Adult specimens of *Leptodactylus savagei* are large (106–164 mm SVL). The toes lack lateral fringes (the toes sometimes have lateral ridges that are not developed into moveable fringes). A single pair of distinct dorsolateral folds is present, and the head is relatively broad. These features are shared with (at least some individuals of) *L. fallax*, *L. flavopictus*, *L. knudseni*, *L. labyrinthicus*, *L. laticeps*, *L. myersi*, *L. paraensis*, *L. pentadactylus*, *L. peritoaktites*, *L. rhodomerus*, *L. stenodema*, *L. turimiquensis*, and *L. vastus*. *Leptodactylus flavopictus* has a dis-



**FIGURE 3.** Wave form and audiospectrogram display of the advertisement call of *Leptodactylus savagei*, USNM recording 89 cut 6. Wave form of first call in audiospectrogram. Recording by Roy W. McDiarmid, Rincon de Osa, Puntarenas, Costa Rica, 11 June 1973, 20:35 h, 74–76°F (no specimen voucher).

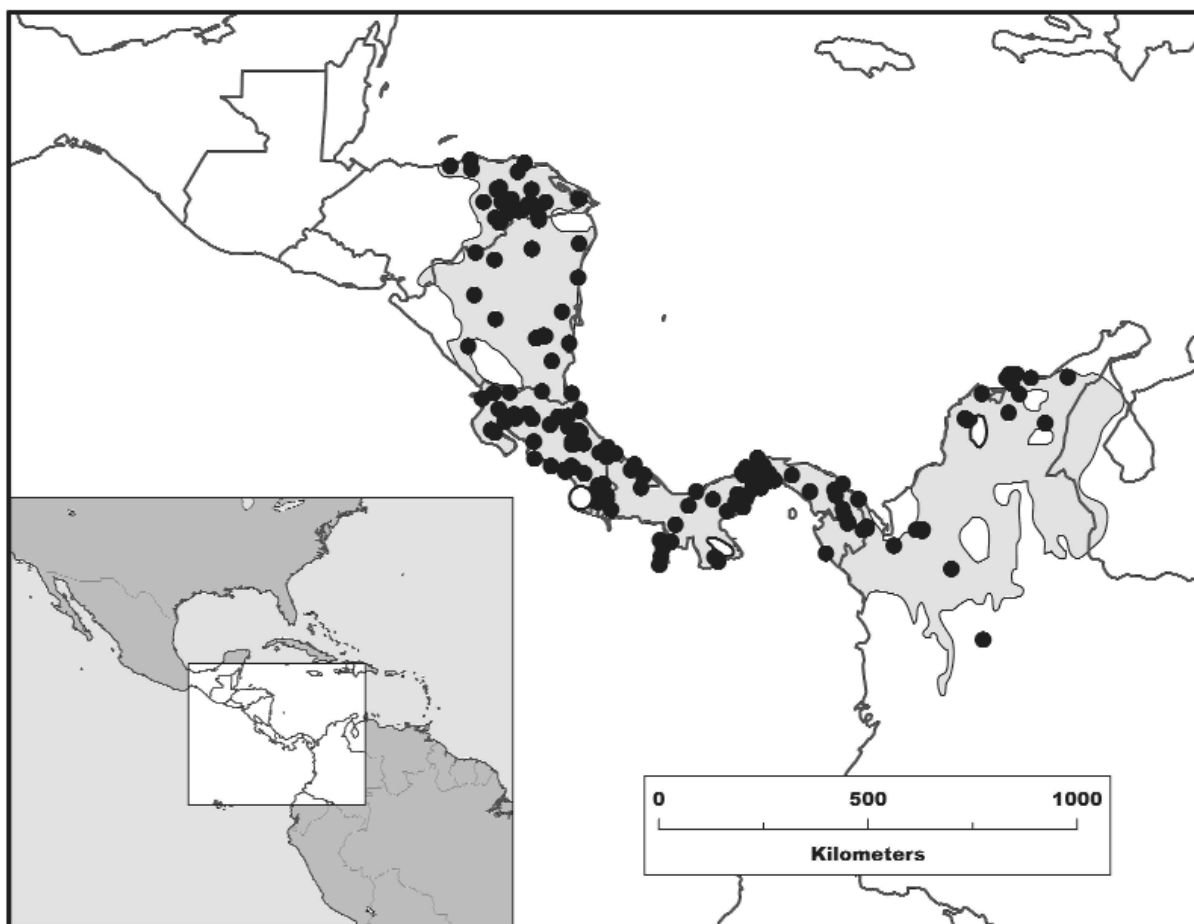
tinct light stripe on the upper lip, whereas *L. savagei* lacks a lip stripe. *Leptodactylus laticeps* has a distinct tile-like dorsal pattern of black squares and rectangles with whitish areas within and between the black markings (in life the black squares and rectangles each have a red center and are separated from one another by a yellow background), whereas *L. savagei* does not have a tile-like dorsal pattern. The dorsolateral folds of *L. savagei* originate just behind the eye and extend above the tympanum toward the sacrum, whereas the dorsolateral folds of *L. stenodema* originate posterior to the tympanum. The dorsolateral folds of *L. savagei* are almost always entire, whereas the dorsolateral folds of *L. labyrinthicus*, *L. myersi*, *L. paraensis*, *L. turimiquensis*, and *L. vastus* usually have interrupted dorsolateral folds or lack dorsolateral folds altogether. Female, sub-adult, and juvenile male *L. savagei* cannot consistently be differentiated morphologically from *L. fallax*, *L. knudseni*, *L. pentadactylus*, *L. peritoaktites*, or *L. rhodomerus*. Adult male *L. savagei* have a pair of chest spines, whereas *L. fallax*, *L. pentadactylus*, and *L. rhodomerus* males lack chest spines. Adult specimens of *L. savagei* cannot be distinguished from adult *L. knudseni*. Larval *L. savagei* have 9 filter rows per plate on ceratobranchial IV, whereas *L. knudseni* larvae have 7 rows. Juvenile *L. savagei* are never green in life, whereas juvenile *L. knudseni* are often green. *Leptodactylus savagei* is the only species being compared that occurs in Middle America. *Leptodactylus savagei* also occurs on the Caribbean versant of Colombia.

• **DESCRIPTIONS.** Heyer (2005) provides a comprehensive description of the holotype of *L. savagei*. Other detailed descriptions of adults may be found in Heyer (1970 [1968], as *L. pentadactylus*, 2005), Savage (2002, as *L. pentadactylus*), and Taylor (1952, as *L. pentadactylus dengleri*). Larval descriptions are in Heyer (1970 [1968], as *L. pentadactylus*, 2005), and Savage (2002, as *L. pentadactylus*). Recordings of the advertisement call of *L. savagei* appear on compact discs by Bradbury and Budney (2001, as *L.*

*pentadactylus*) and Ibáñez D. et al. (1999b, as *L. pentadactylus*). Advertisement call characterizations are provided by Heyer (2005) and Straughan and Heyer (1976, Costa Rica and Panama examples only, as *L. pentadactylus*).

• **ILLUSTRATIONS.** The following photographs or illustrations of *L. savagei*, unless noted by (\*), were referred to by the authors as *L. pentadactylus*: Albert et al. (2005), Bartlett (1996), Buitrago Vannini (2003), Card (1995), Cuentas Montalvo et al. (2002), De la Riva (1997b), Guyer and Donnelly (2004 [2005], as Smoky Jungle Frog), Hawley (2008\*), Henderson (2002, as Smoky Jungle Frog), Heyer (1970 [1968]), Heyer (2005\*), Höbel (2004b, 2008), Ibáñez D. et al. (1999b), Köhler (2001), Krywicki (2001), Leenders (2001), Martínez Cortés and Rodríguez (2005), McCranie and Castañeda (2007a\*), McCranie et al. (2006), McCranie and Wilson (2002), Mendez (1987), Noble (1918), Norman (1998), Park (1938), Pröhl (1997), Renjifo and Lundberg (1999), Rodríguez A. et al. (2005 [2004]), Ryan (1985), Savage (2002), Scott (1983), Taylor (1952, as *L. pentadactylus dengleri*), van Santen (2006), Villa (1972), Villa et al. (1988), Vinton (1938, genus omitted, as Smoky and Smoky Jungle Frog), and Wainwright (2000).

Other illustrations include the following: **audiospectrograms** (Bernal et al. 2007; Heyer 1979, 2005\*; Ibáñez D. et al. 1999a; Kime et al. 2000; Wollerman and Wiley 2002), **defensive behavior** (Villa 1969 [1967], 1972), **foam nests** (Breder 1946; Heyer and Rand 1977; Mertens 1960), **habitat** (Cuentas Montalvo et al. 2002; McCranie and Castañeda 2007a\*), **morphology** (Bhaduri 1953), **photomicrographs of the female urogenital system** (Burton 1998a), **palmar and dorsal musculature of the hand** (Heyer 1969b), **dorsal and ventral views of the skull** (Larson and de Sá 1998), **suprarrostral cartilages, dorsal, ventral, and lateral views of the chondrocranium, ventral view of the hyobranchial apparatus** (Leenders 2001), **male secondary sexual characteristics** (Lynch 1971; Savage 2002; Villa 1972), **maxilla-ptyergoid articulation, dorsal, ventral, lateral, and median views of the right septomaxilla, posterior and dorsal views of the skull, vertebral column, middle ilium, thumb bones, and prepolices of male** (Norman 1998), **upper lip** (Taylor 1952), **lateral head view, thumb spine** (Vinton 1938, as Smoky and Smoky Jungle Frog, x-ray of abdomen with prey), **oocytes** (Davidson and Hough 1969), **larvae** (Breder 1946; Heyer 1970 [1968]; Kluge 1981; Savage 2002; Villa 1972). Altig et al.



**MAP.** Distribution of *Leptodactylus savagei*. The type-locality is indicated by a circle. A dot may represent more than one site. Predicted distribution modified from a BIOCLIM analysis. Published locality data used to generate the map should be considered as secondary sources of information, as we did not confirm identifications for all specimen localities. The locality coordinate data and sources are available on a spread-sheet at <http://learning.richmond.edu/Leptodactylus>.



(2007) provided an illustration of a tadpole preying on a smaller tadpole.

• **DISTRIBUTION.** *Leptodactylus savagei* occurs in mesic areas of Honduras, Nicaragua, Costa Rica, Panama and scattered localities in the Caribbean versant of Colombia, from sea level to 1385 m. The following references to distribution, localities, and altitude when provided, are organized by country; all references listed referred to this species as *Leptodactylus pentadactylus* unless indicated by (\*). **(S)** indicates a secondary source: **Colombia** (Acosta-Galvis et al. 2006\*; Bernal and Lynch 2008\*; Cuentas Montalvo et al. 2002; Renjifo and Lundberg 1999; Romero-Martínez et al. 2008\*; Ruthven 1922), **Costa Rica** (Abella et al. 2008; Albert et al. 2005; Barquero Rodríguez 1994; Barquero Rodríguez and Barquero Arroyo 2007\*; Bartlett 1996; Blankenship 1992; Bringsøe 2003, 2004; Card 1995; Darst and Cannatella 2004; Donnelly 1994; Donnelly and Guyer 1994; Duellman 1967b; Franzen 1988; Gans 1958; Günther 1900, 1902; Guyer and Donnelly 2004 [2005]; Hartdegen et al. 1999; Hawley 2008\*; Hayes et al. 1989; Heatwole and Sexton 1966; Henderson 2002; Heyer 1967, 1970 [1968], 1979, 2005\*; Heyer et al. 1975; Höbel 2000, 2008; Hödl 1996; Johanboeke 1974, 1977 [1976]; Kratzer et al. 1990; Kubicki 2008; Krywicki 2001; Laurencio 2009\*; Leenders 2001; Lewis 2001; Lieberman 1986; Lips and Savage 1996; Malmström 1993; McDiarmid and Savage 2005; Minton and Smith 1960; Norman 1998; Palmer 1992; Pounds 2000 (as Smoky Jungle Frog); Pounds and Fogden 2000; Pounds et al. 1997; Pröhl 1997; Roberts 1997; Sasa and Solórzano 1995; Savage 1973a,b, 1980a,b,c, 2002; Savage and Villa 1986; Scott 1983; Scott and Starrett 1974; Scott et al. 1983; Straughan and Heyer 1976; Taylor 1952, p. 589 **(S)**, p. 651 [as *L. pentadactylus dengleri*]; Valerio 1971; Villa 1969 [1967]; Villa et al. 1982; Wainwright 2000; Wassersug and Heyer 1988; Weimer et al. 1994; Weimer et al. 1993a,b; Wollerman and Wiley 2002; Zelmer and Brooks 2000), **Honduras** (Heyer 1979; House et al. 2002; Köhler et al. 2000; Lynch and Fugler 1965 (as *L. pentadactylus dengleri*); McCranie 2006\*, 2007\*; McCranie and Castañeda 2007a,b; McCranie et al. 2002; McCranie et al. 2006; McCranie and Wilson 2002; Meyer 1969; Meyer and Wilson 1971; Nicholson et al. 2000; Wilson 1983; Wilson and McCranie 1994, 2004 [2003]; Wilson et al. 2001; Wilson and Townsend 2006), **Nicaragua** (Brattstrom and Howell 1954; Buch 1994; Buitrago Vannini 2003; Gaige et al. 1937; Heyer 1979; Köhler 1998, 1999, 2001; Köhler and Seipp 1998; Noble 1918; Villa 1971, 1972, 1983), **Panama** (Asociación Nacional para la Conservación de la Naturaleza (ANCON) and The Nature Conservancy (TNC) 1995a,b, 1996a,b; Barbour 1923; Bernal 2006; Bernal et al. 2007; Bhaduri 1953; Brattstrom 1961, 1968; Breder 1925, 1927, 1946; Brem and Lips 2008\*; Caballero y C. 1955; Cabrera-Gúzman et al. 2007 (p. 97 only); Cedeño et al. 2006; Davidson and Hough 1969; De la Riva 1997a,b; de Sá et al. 2006 [2005]; Dieguez et al.

2006; Dunn 1931a,b, 1933b; Gray and Rand 1997; Heyer 1979; Heyer and Rand 1977; Ibáñez D. et al. 1995 [1994], 1997 [1995], 1999a,b, 2001; Jaeger and Hailman 1981; Jaramillo et al. 1994; Kaufmann 1962; Kluge 1981; Kourany et al. 1970; Leigh 2002; Lips et al. 2003, 2006; Martínez Cortés and Rodríguez 2005; Mendez 1987; Muedeking and Heyer 1976; Myers and Rand 1969; Nemuras 1968; Park 1938; Park et al. 1940; Ponssa 2005 [2004]; Rand and Myers 1990; Rodríguez A. et al. 2005 [2004]; Schmidt 1933; Sexton et al. 1964; Sousa and Arosemena 1991; Summers 2002; Swanson 1945; Tejera Nuñez and Dupuy Loo 1994, 2003; Vinton 1938, 1951; Weaver and Bauer 2004; Wells 1979; Young et al. 1999; Zetek and Wetmore 1951).

• **FOSSIL RECORD.** None.

• **PERTINENT LITERATURE.** Inclusive accounts of the species are found in Heyer 2005, McCranie and Wilson 2002 (as *L. pentadactylus*), and Savage 2002 (as *L. pentadactylus*). The following literature is listed by topic; all references listed referred to this species as *Leptodactylus pentadactylus* unless indicated by (\*), which signifies *L. savagei*. The symbol **(M)** indicates the species is only mentioned and **(S)** indicates that all the species information represents a secondary source: **bibliographic information and lists** (Campbell 1999; Cochran 1940 [Vinton 1938 reference only]; Hardouin 1997; Liner 1994 [Sexton et al. 1964 reference only], 1997, 1998, 2009; Liner and Gans 2004; Lips and Savage 1996; Savage 1980a,c, 2002; Savage and Villa 1986 [p. 23, Heyer 1970b, as CR spp., Scott 1983m as *L. pendactylus* {sic}, and p. 104 as *L. pentadactylus* {sic}]; Toledo et al. 2007 **(S)** [Roberts 1997a citation only; Villa et al. 1988 [except Breen 1974, Cochran and Goin 1970, Duellman 1978, Duellman and Trueb 1986, and most information in Heyer 1979 except Central American localities]; Vizotto 1964 [p. 389 only]; Walley 1997), **biogeography** (Lynch 1971; Maxson and Heyer 1982; Wilson and McCranie 1998), **book reviews and articles** (Eckerlin 1971; Wilson and Meyer 1972), **call and call parameters** (Aycrigg et al. 1998 **(S)**; Bernal 2006; Bernal et al. 2007; Breder 1927, 1946; Duellman 1967a; Duellman and Trueb 1966; Dunn 1933a, b; Fouquette 1960; Gray and Rand 1997; Höbel 2008; Johanboeke 1974, 1977 [1976]; Kime et al. 2000; Kluge 1981 **(S)**; LeVering 1999 [p. 52 and as experimental animal throughout]; Park 1938; Park et al. 1940; Rose et al. 1988; Ryan 1985; Scott and Limerick 1983; Straughan and Heyer 1976 [p. 228, Costa Rican and Panamanian information, and p. 232; Toledo and Haddad 2009\*; Wollerman and Wiley 2002; Zelick et al. 1991), **checklists** (Abella et al. 2008; Auth 1994; Bernal and Lynch 2008\*; Burger 2001; Leenders 2001; McDiarmid and Savage 2005; Myers and Rand 1969; Palmer 1992; Savage 1973a, b, 1980b; Savage and Bolaños 2009\*; Savage and Villa 1986; Scott et al. 1983; Villa 1971, 1983), **conservation** (Asociación Nacional para la Conservación de la Naturaleza (ANCON) and The Nature Con-

- servancy (TNC) 1995a,b, 1996a,b; Dieguez et al. 2006; McCranie et al. 2006; McCranie and Wilson 2002; Weimer et al. 1994; Wilson and McCranie 2004 [2003]; Wilson and Townsend 2006; Young et al. 1999), **development** (Barquero Rodríguez and Barquero Arroyo 2007\*; Blankenship 1992; Breder 1946; Gallardo 1958; Savage 2002; Vinton 1951; Vizotto 1967 (S)), **dictionaries and encyclopedias** (Marx and Heath 1992 (as burka and la rana mugidora come-pollo)), **distribution** (Campbell 1999; Cei 1968 [as *L. pentadactylus dengleri*]; Lynch and Fugler 1965 (S); McCranie et al. 2006; McCranie and Wilson 2002; Meyer 1969), **ecology, natural history, reproduction** (Alford 1999 (S); Altig 1974 [1972]; Altig and McDiarmid 2007; Altig et al. 2007; Barbour 1923; Barlow 1998 (S) [Heyer et al. 1975 citation only]; Barquero Rodríguez 1994; Behler and Behler 2005 [p. 52 only]; Bernal 2006; Bernal et al. 2007; Borteiro and Kolenc 2007 (S); Brattstrom and Howell 1954; Breder 1925, 1927, 1946; Brodie et al. 1978 (S); Caldwell 1992 (S); Card 1995; Cardoso and Sazima 1997 (S); Conzernius 1932 [as burka and burki]; Cooke 1984; Cooke et al. 2008; Cramer et al. 2001 (S); Crossland 1998 (S); Crossland and Azevedo-Ramos 1999 (S); Crump 1992 (S); Cuentas Montalvo et al. 2002; Davidson and Hough 1969; De la Riva 1993 [p. 109 Muedeking and Heyer 1976, citation only, and p. 110 1997a,b]; Dent 1956 (S); Dixon et al. 1993; Donnelly 1994; Downie 1984 (S); Downie et al. 1995; Downie and Smith 2003 (S); Duellman 1966; Duellman and Trueb 1966, 1986 [pp. 75 (S), 162 (S), 244 (S), 273 (S), 281 (S); Dunn 1954; Gibson and Buley 2004 [p. 133 Hödl citation only], Green 1990; Greene 1988, 1997; Gregory 1983 (S); Gunzburger and Travis 2005 [p. 561 Heyer et al. citations only, and pp. 563 and 570 only]; Heyer 1967; Heyer et al. 1975; Heyer and Rand 1977; Heyer and Scott 2006 (S); Höbel 2000, 2004a,b, 2008; Hödl 1988 (S), 1990a (S), b (S) [Breder 1946 and Heyer and Rand 1977 citations only], 1992 (S); Ibáñez D. et al. 1997 [1995], 1999a; Jaeger 1978 (S); Jaeger and Hailman 1981; Johannecke 1974, 1977 [1976]; Kaufmann 1962; Kluge 1981; Kotiaho 2001 (S); Kubicki 2008; Lebron et al. 1995 (S); Leigh 2002; LeVering 1999 [p. 52 and as experimental animal throughout]; Lieberman 1986; Lips et al. 2003; Lutz 1947 (S); Malkin 1956; Magnhagen 1991 (S); Manzanilla Puppo et al. 2005 (S); McCranie et al. 2006; McCranie and Wilson 2002; Meyer 1969; Mudde and van Dijk 1983; Muedeking and Heyer 1976; Nemuras 1968; Noble 1918, 1927; Park 1938; Petranks et al. 1994 (S); Petranks and Kennedy 1999 (S); Polis and Myers 1985 (S); Ponssa 2005 [2004]; Ponssa and Barrionuevo 2008\*; Pough et al. 1996 (S); Pounds 2000 (S) [as Smoky Jungle Frog]; Prado et al. 2005 (S) [Vinton 1951 and Muedeking and Heyer 1976 citations only]; Prado et al. 2002 (S) [Breder 1946, Heyer et al. 1975, Muedeking and Heyer 1976, and Vinton 1951 citations only]; Rand 1983 [p. 412], Rand and Myers 1990; Roberts 1997; Rodrigues et al. 2007 (S)\*; Rodrigues et al. 2005 [2004] (S); Roth and Willis 1960; Noble 1918; Ruibal and Thomas 1988 (S); Ryan 1985; Ryan and Tuttle 1983 (S); Ryan et al. 1981; Sasa and Solórzano 1995; Savage 2002; Scott and Limerick 1983 [Breder 1946, Villa 1967, 1972, and Vinton 1951 citations only]; Sherratt and Harvey 1989 (S); Silva and Juncá 2006 (S); Silva and Giaretta 2009\*; Silva et al. 2005 (S) [Heyer and Rand 1977 and Muedeking and Heyer 1976 citations only]; Tárano 1998; Tejedo 1991 (S); Toft 1985 (S); Toft et al. 1982 (S); Toledo et al. 2007 (S) [p. 172 only]; Toledo et al. 2005 (S) [Villa 1969 citation only]; Tuttle and Ryan 1981; Veloso 1977 (S); Vera Candioti 2004, 2005 (S), 2006 (S); Villa 1969 [1967], 1972; Villa et al. 1982 [Costa Rican example and Muedeking and Heyer 1976 citations only]; Vinton 1938, 1951; Vizotto 1967 (S); Wassersug and Heyer 1988; Wells 1979, 2007 (S) [pp. 293, 341, 573, 661, 663 only]; Wilson and McCranie 2004 [2003]; Wilson et al. 2001; Wunder 1932 (S); Zelick et al. 1991; Zina and Haddad 2005 (S)), **evolution** (Heyer 1969a [Breder 1946 citation only]; Heyer and Liem 1976 (S); Lynch 1971; Silva and Giaretta 2009\*), **faunal lists** (Mendez 1987; Park et al. 1940; Zetek and Wetmore 1951), **field guides** (Beletsky 1998 [except plate 4, as Smoky Jungle Frog]; De la Riva 1997b; Henderson 2002; Leenders 2001; McCranie and Castañeda 2007a\*; Norman 1998; Renjifo and Lundberg 1999; Wainwright 2000), **habitat** (Acosta Galvis et al. 2006\*; Asociación Nacional para la Conservación de la Naturaleza (ANCON) and The Nature Conservancy (TNC) 1995a,b, 1996a,b; Burger 2001; Campbell 1999; Cuentas Montalvo et al. 2002; Dunn 1931a, 1933b; House et al. 2002; Ibáñez D. et al. 1995 [1994], 1997 [1995], 1999a; Kubicki 2008\*; Laurencio 2009\*; Lieberman 1986; McCranie et al. 2006; McCranie and Wilson 2002; Park 1938; Pounds and Fogden 2000; Pounds et al. 1997; Rand and Myers 1990; Ruthven 1922; Sasa and Solórzano 1995; Savage 2002; Sexton et al. 1964; Tejera Nuñez and Dupuy Loo 2003; Wells 2007 (S) [p. 98 only]; Wilson and McCranie 1998; Wilson et al. 2001; Wilson and Townsend 2006), **inventories** (Asociación Nacional para la Conservación de la Naturaleza (ANCON) and The Nature Conservancy (TNC) 1995a,b, 1996a,b; Cedeño et al. 2006; De La Riva 1997a; Laurencio 2009\*; Lewis 2001; McCranie et al. 2002; Nicholson et al. 2000; Rodríguez A. et al. 2005 [2004]), **karyotypes** (Morescalchi 1973 (S); Morescalchi and Gargiulo 1968; Rabello 1970 (S) [Morescalchi and Gargiulo citations only]); **keys** (Breder 1946; Cuentas Montalvo et al. 2002; Dunn 1931a; Guyer and Donnelly 2004 [2005]; Heyer 1970 [1968]; Köhler 1999, 2001; Lips and Savage 1996; McCranie and Castañeda 2007a\*; McCranie et al. 2006; McCranie and Wilson 2002; Meyer and Wilson 1971; Nemuras 1968; Romero-Martínez et al. 2008\*; Savage 1980a, c, 2002; Savage and Villa 1986; Taylor 1952 [as *L. pentadactylus dengleri*]; Villa 1972; Wilson and McCranie 1993), **lists of specimens in collections** (Cope 1887; Tejera Nuñez and Dupuy Loo 1994, 2003), **miscellaneous mention** (Jara 2008a,b; Jungfer 1988; Mudde and van Dijk 1985; Vizotto 1984 (S)), **morphology** (Bhaduri 1953; Burton



1998a,b, 2004; Cardozo 2004 (**S**); Fabrezi and Vera 1997; Fox 1984 (**S**); Goin 1959 [as *L. pentadactylus dengleri*]; Hayek and Heyer 2005; Jaslow 1985, 1987; Johanboeke 1977 [1976]; Kluge 1981; Larson and de Sá 1998; Lynch 1971; McCranie and Wilson 2002; Miranda and Ferreira 2008 (**S**) [Wassersug and Heyer 1988 citation]; Muedeking and Heyer 1976; Palavecino 1997 (**S**); Prado and d'Heursel 2006 (**S**); Rodrigues et al. 2007 (**S**)\*; Savage 2002; Scott and Limerick 1983; Silva and Mendelson 1999; Starrett 1968 [Costa Rican specimens only]; Vera Candioti 2006 (**S**); Vera Candioti et al. 2007 [Larson and de Sá 1998 and Wassersug and Heyer 1988 information only]; Vieira et al. 2007 (**S**) [Muedeking and Heyer 1976, Savage 2002, Vizotto 1967, Wassersug and Heyer 1988, and Central American *L. pentadactylus* citations only]; Villa 1972; Villa et al. 1982 (**S**) [Villa 1969, 1972 citations only]; Wassersug and Heyer 1988; Wells 2007 (**S**) [pp. 577 and 661 only]), **nomenclature and taxonomy** (McCranie and Wilson 2002; Smith 1987), **parasites and diseases** (Brem and Lips 2008\*; Caballero y C. 1955; Cabrera-Guzmán et al. 2007 [p. 97 only]; Duellman and Trueb 1986 [p. 243 only]; Hartdegen et al. 1999; Johnston 1975 [p. 530 only]; Kourany et al. 1970; Lamothe-Argumedo and Jaimes Cruz 1982; Lamothe-Argumedo et al. 1997; Lips et al. 2006; Metcalf 1923 [p. 408 only, Panamanian specimen]; Suriano 1970 [p. 218 only]\*; Taylor et al. 2001 (**S**) [Kourany et al. 1970 citation only]; Thatcher 1993 [p. 183 only]; Villa 1984 (**S**) [Villa et al. 1982 citation only]; Villa et al. 1982 [Costa Rican example and Muedeking and Heyer 1976 citation only]; Wells 2007 (**S**) [p. 835 only]\*; Yamaguti 1971 [p. 341 only]; Zelmer and Brooks 2000 [p. 1114, column 1 only]), **physiology** (Brattstrom 1961, 1968; Valerio 1971), **popular literature** (Archer 2006; Bartlett 1988, 1996; Behler and Behler 2005 [pp. 52 and 105 only]; Echternacht 1977; Mendez 1987; Nemuras 1976; Pröhl 1997; Tuttle 1982; Vinton 1938), **relationships, systematics and phylogeny** (Austin et al. 2002; Ceï et al. 1967 [as *L. pentadactylus dengleri*]; Darst and Cannatella 2004; de Sá et al. 2006 [2005]; Dutta et al. 2004; Grant et al. 2006; Graybeal 1997; Hedges et al. 2008; Hedges and Heinicke 2007; Heinicke et al. 2007; Heyer 1995, 1998; Heyer and Maxson 1982 [p. 401 figure 6 as *L. pentadactylus*, Panama only]; Larson and de Sá 1998; Larson et al. 2003; Leistikow 2001 (**S**); [as Costa Rican population of *L. pentadactylus*]; Lourenço et al. 2008 (**S**); Lynch 1971; Maxson and Heyer 1982, 1988 [antigen sample from Panama only]; Miyamoto 1981; Ponssa and Barrionuevo 2008\*, Wassersug and Heyer 1988), **skin secretions** (Anastasi et al. 1970 [as *L. pentadactylus dengleri*]; Ceï 1969 [as *L. pentadactylus dengleri*], 1972, 1980 [both as *L. dengleri*]; Ceï and Erspamer 1965, 1966 [both as *L. pentadactylus dengleri*]; Ceï et al. 1967 [as *L. pentadactylus dengleri*]; G. Erspamer and Ceï 1970 [as *L. pentadactylus dengleri*]; V. Erspamer 1971 [as *L. pentadactylus dengleri*]; V. Erspamer et al. 1963 [as *L. pentadactylus dengleri*]; Erspamer and Erspamer 1965 [as *L. pentadactylus dengleri*]; V. Erspamer et

al. 1986 [as *L. pentadactylus dengleri*]; V. Erspamer et al. 1964 [p. 1089 only as *L. pentadactylus dengleri*]; V. Erspamer et al. 1964, 1967 [both as *L. pentadactylus dengleri*]; Flier et al. 1980; Roseghini et al. 1986) [as *L. pentadactylus dengleri*], **species accounts** (Albert et al. 2005; Beletsky 1998; Buitrago Vannini 2003; Cuentas Montalvo et al. 2002; Günther 1900; Henderson 2002; Heyer 1970 [1968], 2005\*; Ibáñez D. et al. 1999a [see Heyer et al. in prep. *Leptodactylus pentadactylus* for clarification of references in this species account]; Köhler 1999, 2001; Leenders 2001; Martínez Cortés and Rodríguez 2005; McCranie and Castañeda 2007a\*; McCranie et al. 2006; McCranie and Wilson 2002; Mendez 1987; Noble 1918; Norman 1998; Pröhl 1997; Renjifo and Lundberg 1999; Rodríguez A. et al. 2005 [2004]; Savage 2002; Scott 1983 [Heyer 1979 citation]; Taylor 1952 [as *L. pentadactylus dengleri*]; Villa 1972; Weimer et al. 1993b), **species comparisons** (Dunn 1940; Heyer 2005 [as Middle American Unit]; Heyer and Heyer 2006 [as undescribed species from Middle America]; Savage 2002; Skuk et al. 2007; Vieira et al. 2007 (**S**) [Muedeking and Heyer 1976, Savage 2002, Vizotto 1967, Wassersug and Heyer 1988, and Central American *L. pentadactylus* citations only]; Villa 1972; Wassersug and Heyer 1988), **species or taxonomic lists** (Cuentas Montalvo et al. 2002; Dunn 1931b; Gans 1958 [as *L. pentadactylus pentadactylus*]; Hayes et al. 1989; House et al. 2002; Ibáñez D. 2005; Ibáñez D. et al. 1995 [1994], 1997 [1995], 1999a, 2001; Köhler 1999, 2001; Köhler et al. 2000; Köhler and Seipp 1998; Krywicki 2001; Kubicki 2008\*; Laurencio 2009\*; Lewis 2001; Malmström 1993; Martínez Cortés and Rodríguez 2005; McCranie and Castañeda 2007b; Noble 1918; Pounds et al. 1997; Romero-Martínez et al. 2008\*; Ruiz Pérez and Buitrago Vannini 2003; Schmidt 1933; Sousa and Arosemena 1991; Villa 1972; Weaver and Bauer 2004; Weimer et al. 1994; Weimer et al. 1993a; Wilson 1983; Wilson and McCranie 1994, 1998, 2004 [2003]; Wilson et al. 2001; Wilson and Townsend 2006; Young et al. 1999).

• **REMARKS.** The following common names have been published for *Leptodactylus savagei*: “Savage’s Thin-toed Frog” proposed English common name at [www.learning.richmond.edu/Leptodactylus](http://www.learning.richmond.edu/Leptodactylus), “Rã-de-dedos-delgados-de-Savage” proposed Portuguese common name at [www.learning.richmond.edu/Leptodactylus](http://www.learning.richmond.edu/Leptodactylus), and “Rana de dedos delgados de Savage” proposed Spanish common name at [www.learning.richmond.edu/Leptodactylus](http://www.learning.richmond.edu/Leptodactylus). Other cited common names are as follows; all references listed referred to this species as *Leptodactylus pentadactylus* unless otherwise indicated: **Bürh** (Green 1999), **Burka** (Conzernius 1932; House et al. 2002; Marx and Heath 1992; McCranie et al. 2006), **Burkxá** (Malkin 1956), **Central American Bullfrog** (Greene 1997; Guyer and Donnelly 2004 [2005]; Leenders 2001; Martínez Cortés and Rodríguez 2005), **La Rana Mugidora Come-Pollo** (Marx and Heath 1992), **Rana Comepollos** (Guyer

and Donnelly 2004 [2005]), **Rã de-dedos-delgados-de-Savage** (Heyer 2005, as *L. savagei*), **Rana de-dedos delgados de Savage** (Heyer 2005, **Rana Grande de la Selva** (McCrane and Castañeda 2007a, as *L. savagei*), **Rana Ternerero** (Barquero Rodríguez and Barquero Arroyo 2007 [as *L. savagei*]; Beletsky 1998; Buitrago Vannini 2003; Burger 2001; Guyer and Donnelly 2004 [2005]; Köhler 1999, 2001; Leenders 2001; Norman 1998; Pröhl 1997; Savage 2002; Villa 1969 [1967], 1971, 1972, 1983; Villa et al. 1988; Wainwright 2000), **Rana Toro** (Beletsky 1998; Cedeño et al. 2006; Höbel 2008; Leenders 2001; Pröhl 1997; Rodríguez A. et al. 2005 [2004]), **Savage's Thin-Toed Frog** (Heyer 2005 as *L. savagei*), **Smoki Jungle Frog** (Savage 2002), **Smoky** (Vinton 1938), **Smoky Frog** (Beletsky 1998), **Smoky Jungle Frog** (Bartlett 1988, 1996; Behler and Behler 2005, p. 52 only); Beletsky 1998; Bernal 2006; Blankenship 1992; Burger 2001; Cochran 1940 [Vinton 1938 reference only]; Guyer and Donnelly 2004 [2005]; Hayes et al. 1989; Henderson 2002; Krywicki 2001; Lewis 2001; Norman 1998; Pounds 2000; Roth and Willis 1960; Vinton 1938, 1951; Wainwright 2000), **South American Bullfrog** (Beletsky 1998; Green 1990; Guyer and Donnelly 2004 [2005]; Höbel 2008; Hödl 1992; Johanboeke 1974, 1977 [1976]; Leigh 2002; Lewis 2001; Ryan 1985; Tárano 1998; Tuttle 1982); **Südamerikanische Ochsenfrosch** (Hödl 1996); **Sukli'n** (Malkin 1956).

• **ETYMOLOGY.** *Leptodactylus savagei* honors Dr. Jay M. Savage whose work in Costa Rican herpetology has inspired countless researchers and promoted a comprehensive understanding of the Costa Rican herpetofauna.

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## LITERATURE CITED

- Abella, I., R. Gómez, and M. López. 2008. Annotated amphibian and reptiles check-list of Pacuare Nature Reserve, Costa Rica. *Boletín de la Asociación Herpetológica Española* 19:64–67.
- Acosta-Galvis, A.R., C. Huertas-Salgado, and M. Rada. 2006. Aproximación al conocimiento de los anfibios en una localidad del Magdalena medio (Departamento de Caldas, Colombia). *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 30:291–303.
- Albert, R., W. Hödl, W. Huber, M. Ringler, P. Weish, and A. Weissenhofer. 2005. The Amphibians and Reptiles of the Golfo Dulce Region Costa Rica: Corcovado National Park, Piedras Blancas National Park, "Regenwald der Österreicher". W. Huber & A. Weissenhofer, Vienna.
- Alford, R.A. 1999. Ecology. Resource use, competition, and predation, p. 240–278. *In* R.W. McDiarmid, and R. Altig (eds.), *Tadpoles: The Biology of Anuran Larvae*. The University of Chicago Press, Chicago.
- Altig, R. 1974 (1972). Defensive behavior in *Rana areolata* and *Hyla avivoca*. *Quarterly Journal of the Florida Academy of Sciences* 35:212–216.
- and R.W. McDiarmid. 2007. Morphological diversity and evolution of egg and clutch structure in amphibians. *Herpetological Monographs* 21:1–32.
- , M.R. Whiles, and C.L. Taylor. 2007. What do tadpoles really eat? Assessing the trophic status of an understudied and imperiled group of consumers in freshwater habitats. *Freshwater Biology* 52:386–395.
- Anastasi, A., G. Bertaccini, J.M. Cej, G. De Caro, V. Erspamer, M. Impicciatore, and M. Roseghini. 1970. Presence of caerulein in extracts of the skin of *Leptodactylus pentadactylus labyrinthicus* and of *Xenopus laevis*. *British Journal of Pharmacology* 38:221–228.
- Archer, J. 2006. Program notes from the August CHS meeting. *Bulletin of the Chicago Herpetological Society* 41:171.
- Asociación Nacional para la Conservación de la Naturaleza (ANCON) and The Nature Conservancy (TNC). 1995a. Ecological Survey of the U.S. Department of Defense Lands in Panama. Phase II: Albrook Air Force Station, Corozal, Fort Clayton, Fort Amador, Quarry Heights, Semaphore Hill, Summit Radio Station Panama. The Nature Conservancy, Legacy Resource Management, Asociación Nacional para la Conservación de la Naturaleza, Panama City.
- . 1995b. Ecological Survey of the U.S. Department of Defense Lands in Panama. Phase IV: Fort Davis and Fort Gulick, Panama. The Nature Conservancy, Legacy Resource Management, Asociación Nacional para la Conservación de la Naturaleza, Panama City.
- . 1996a. Ecological Survey of the U.S. Department of Defense Lands in Panama. Phase III: HOROKO, Empire Range and Balboa West Range, Panama. The Nature Conservancy, Legacy Resource Management, Asociación Nacional para la Conservación de la Naturaleza, Panama City.
- . 1996b. Ecological Survey of the U.S. Department of Defense Lands in Panama. Phase IV: Fort Sherman, Piña Range and Naval Security Group Activity, Galeta Island, Panama. The Nature Conservancy, Legacy Resource Management, Asociación Nacional para la Conservación de la Naturaleza, Panama City.
- Austin, J.D., S.C. Loughheed, K. Tanner, A.A. Chek, J.P. Bogart, and P.T. Boag. 2002. A molecular perspective on the evolutionary affinities of an enigmatic neotropical frog, *Allophryne ruthveni*. *Zoological Journal of the Linnean Society* 134:335–346.
- Auth, D.L. 1994. Checklist and bibliography of the amphibians and reptiles of Panama. *Smithsonian Herpetological Information Service* (98):1–59.
- Aycrigg, A.D., T.M. Farrell, and P.G. May. 1998. SOS: Sounds of survival. *Reptile & Amphibian Maga-*

- zine 1998:56–63.
- Barbour, T. 1923. Notes on reptiles and amphibians from Panama. Occasional Papers of the Museum of Zoology, University of Michigan (129):1–16.
- Barlow, L.A. 1998. The biology of amphibian taste. *Amphibian Biology* 3:743–782.
- Barquero Rodríguez, M. 1994. Hábitos alimenticios de *Leptodactylus pentadactylus* (Laurenti, 1768) en Golfito, Costa Rica. *Brenesia* 41–42:95–97.
- and M.D. Barquero Arroyo. 2007. Desarrollo embrionario de la rana ternero, *Leptodactylus savagei* (Anura: Leptodactylidae). *Brenesia* 68:59–67.
- Bartlett, R.D. 1988. In Search of Reptiles and Amphibians. E.J. Brill, Leiden, New York, København, Köln.
- . 1996. A Costa Rica interlude (part 3). *Reptiles Magazine* 4:24, 26, 28, 30.
- Behler, J.L. and D.A. Behler. 2005. *Frogs: A Chorus of Colors*. Sterling Publishing Co., Inc., New York.
- Beletsky, L. 1998. Costa Rica. The Ecotravellers' Wildlife Guide, Natural World, Academic Press, San Diego, London, Boston, New York, Sydney, Tokyo, Toronto.
- Bernal, M.H. and J.D. Lynch. 2008. Review and analysis of altitudinal distribution of the Andean anurans in Colombia. *Zootaxa* (1826):1–25.
- Bernal, X.E. 2006. *Caiman crocodilus* (Spectacled Caiman). Predation/eavesdropper. *Herpetological Review* 37:460–461.
- , A.S. Rand, and M.J. Ryan. 2007. Sexual differences in the behavioral response of Túngara frogs, *Physalaemus pustulosus*, to cues associated with increased predation risk. *Ethology* 113:755–763.
- Bhaduri, J.L. 1953. A study of the urinogenital system of Salientia. Proceedings of the Zoological Society of Bengal 6:1–111.
- Blankenship, J.R. 1992. Feeding trial of the Smoky Jungle Frog larva (*Leptodactylus pentadactylus*) [Abstract]. Society for the Study of Amphibians and Reptiles, University of Texas at El Paso. August 3–6, 1992:35.
- Borteiro, C. and F. Kolenc. 2007. Redescription of the tadpoles of three species of frogs from Uruguay (Amphibia: Anura: Leiuperidae and Leptodactylidae), with notes on natural history. *Zootaxa* (1638):1–20.
- Bradbury, J.W. and G.F. Budney. 2001. The Diversity of Animal Sounds. Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York.
- Brattstrom, B.H. 1961. Thermoregulation in tropical amphibians. The American Philosophical Society, Year Book 1960:284–287.
- . 1968. Thermal acclimation in anuran amphibians as a function of latitude and altitude. *Comparative Biochemistry and Physiology* 24:93–111.
- and T.R. Howell. 1954. Notes on some collections of reptiles and amphibians from Nicaragua. *Herpetologica* 10:114–123.
- Breder, C.M., Jr. 1925. In Darien jungles. Experiences of a student of reptile and amphibian life in a little-known part of Panama. *Natural History* 25:324–337.
- . 1927. Nests of some tropical frogs. *Zoological Society Bulletin* (New York Zoological Society) 30:71–75.
- . 1946. Amphibians and reptiles of the Rio Chucunaque drainage, Darien, Panama, with notes on their life histories and habits. *Bulletin of the American Museum of Natural History* 86:375–436 + Plates 42–60.
- Brem, F.M.R. and K.R. Lips. 2008. *Batrachochytrium dendrobatidis* infection patterns among Panamanian amphibian species, habitats and elevations during epizootic and enzootic stages. *Diseases of Aquatic Organisms* 81:189–202.
- Bringsøe, H. 2003. Herpetologi i Costa Rica 2. Frøer og tudser i østkystens regnskove. *Nordisk Herpetologisk Forening* 46:98–114.
- . 2004. Herpetologi i Costa Rica 3. Øgler og slanger i østkystens regnskove. *Nordisk Herpetologisk Forening* 47:106–121.
- Brodie, E.D., Jr., D.R. Formanowicz Jr., and E.D. Brodie III. 1978. The development of noxiousness of *Bufo americanus* tadpoles to aquatic insect predators. *Herpetologica* 34:302–306.
- Buch, J. 1994. Rejsefortælling fra Nicaragua. *Nordisk Herpetologisk Forening* 37:69–76.
- Buitrago Vannini, F. 2003. Guía ilustrada de los anfibios de Nicaragua, p. 21–121. In G.A. Ruiz Pérez, and F. Buitrago Vannini (eds.), *Guía Ilustrada de la Herpetofauna de Nicaragua*. ARAUCARIA-MARENA-AECI, Managua.
- Burger, R.M. 2001. The herpetofauna of Caño Palma Biological Station, Tortuguero, Costa Rica. *Bulletin of the Chicago Herpetological Society* 36:243–253.
- Burton, T.C. 1998a. Variation in the hand and superficial throat musculature of neotropical leptodactylid frogs. *Herpetologica* 54:53–72.
- . 1998b. Pointing the way: the distribution and evolution of some characters of the finger muscles of frogs. *American Museum Novitates* (3229):1–13.
- . 2004. Muscles of the pes of hyliid frogs. *Journal of Morphology* 260:209–233.
- Caballero y C., E. 1955. Helminths of the Republica de Panamá. XIII. Una nueva especie de *Catadiscus* Cohn, 1904. (Trematoda: Digenea). *Revista Ibérica de Parasitología* Tomo Extra, Marzo, 1955:23–26 + 2 figures.
- Cabrera-Guzmán, E., V. León-Régagnon, and L. García-Prieto. 2007. Helminth parasites of the leopard frog *Rana* cf. *forreri* (Amphibia: Ranidae) in Acapulco, Guerrero, Mexico. *Comparative Parasitology* 74:96–107.
- Caldwell, J.P. 1992. Diversity of reproductive modes in anurans: facultative nest construction in gladiator frogs, p. 85–97. In W.C. Hamlett (ed.), *Reproductive Biology of South American Vertebrates*. Springer-Verlag, New York.
- Campbell, J.A. 1999. Distribution patterns of amphibians in Middle America, p. 111–210. In W.E. Duellman (ed.), *Patterns of Distribution of Amphibians. A Global Perspective*. The Johns Hopkins University Press, Baltimore.



- Card, W. 1995. Notes on herping in the tropical wet forests of Costa Rica. *The Vivarium* 7:30–37.
- Cardoso, A.J. and I. Sazima. 1977. Batracofagia na fase adulta e larvária da rã pimenta, *Leptodactylus labyrinthicus* (Spix, 1824) - Anura, Leptodactylidae. *Ciência e Cultura* 29:1130–1132.
- Cardozo, O.M. 2004. Cambios Morfológicos Externos y del Cráneo Durante la Metamorfosis de *Leptodactylus mystacinus* (Anura: Leptodactylidae). Licenciado en Ciencias Biológicas, Universidad Nacional de Salta, Salta, Argentina.
- Cedeño, J., V. Martínez Cortés, and H. Fossatti. 2006. Anfíbios en La Reserva Forestal La Tronosa: diversidad y estado de conservación. *Tecnociencia* 8:101–114.
- Cei, J.M. 1968. Distribution et spécialisation des batraciens sudaméricains, p. 199–214. In C. Delamare Deboutteville, and E. Rapoport (eds.), *Biologie de l'Amérique Australe. Volume IV. Documents Biogéographiques et Écologiques*, Éditions du Centre National de la Recherche Scientifique, Paris.
- . 1969. Niveles actuales de aproximación de la sistemática no morfológica. *Acta Zoológica Lilloana* 24:293–307.
- . 1972. Correlación evolutiva de caracteres bioquímicos en un anuro alto-amazónico: *Leptodactylus vilarsi* Melin. *Acta Zoológica Lilloana* 29: 261–269.
- . 1980. Amphibians of Argentina. *Monitore Zoologico Italiano (N.S.)*, Monografía (2):xii + 609 p.
- and V. Eerspämer. 1965. Relaciones taxonómicas y evolución bioquímica de las aminos biógenas en el género *Leptodactylus*. *Investigaciones Zoológicas Chilenas Special*:1–8.
- and —. 1966. Biochemical taxonomy of South American amphibians by means of skin amines and polypeptides. *Copeia* 1966:74–78.
- , —, and M. Roseghini. 1967. Taxonomic and evolutionary significance of biogenic amines and polypeptides occurring in amphibian skin. I. Neotropical leptodactylid frogs. *Systematic Zoology* 16: 328–342.
- Cochran, D.M. 1940. Amphibians, p. 289–292. In B. Altsheler (ed.), *Natural History Index-Guide. An Index to 3,365 Books and Periodicals in Libraries. A Guide to Things Natural in the Field. Where and How to Find the most Important Objects of Natural Interest in all Countries as Described in the Leading Publications by the Popular Authors and Well-known Scientists and Explorers of Various Nationalities*, Second edition. H.W. Wilson Company, New York.
- Conzemius, E. 1932. Ethnographical survey of the Miskito and Sumu Indians of Honduras and Nicaragua. *Bureau of American Ethnology, Smithsonian Institution, Bulletin* (106):vii + 191 p.
- Cooke, R.G. 1984. Archaeological research in central and eastern Panama: a review of some problems, p. 263–302. In F.W. Lange and D.Z. Stone (eds.), *The Archaeology of Lower Central America. A School of American Research Book*, University of New Mexico Press, Albuquerque.
- Cooke, R.G., M. Jiménez, and A.J. Ranere. 2008. Archaeozoology, art, documents, and the life assemblage, p. 95–121. In E.J. Reitz, C.M. Scarry, and S.J. Scudder (eds.), *Case Studies in Environmental Archaeology*, Second Edition. Springer, New York.
- Cope, E.D. 1887. Catalogue of the batrachians and reptiles of Central America and Mexico. *Bulletin of the United States National Museum* (32):1–98.
- Cramer, M.J., M.R. Willig, and C. Jones. 2001. *Trachops cirrhosus*. *Mammalian Species* (656):1–6.
- Crossland, M.R. 1998. Predation by tadpoles on toxic toad eggs: the effect of tadpole size on predation success and tadpole survival. *Journal of Herpetology* 32:443–446.
- and C. Azevedo-Ramos. 1999. Effects of *Bufo* (Anura: Bufonidae) toxins on tadpoles from native and exotic *Bufo* habitats. *Herpetologica* 55:192–199.
- Crump, M.L. 1992. Cannibalism in amphibians, p. 256–276. In M.A. Elgar and B.J. Crespi (eds.), *Cannibalism: Ecology and Evolution Among Diverse Taxa*. Oxford University Press, Oxford, New York.
- Cuentas Montalvo, D., R. Borja Acuña, J.D. Lynch, and J.M. Rengifo [sic]. 2002. Anuros del Departamento del Atlántico y Norte de Bolívar. *Cencys* 21, Barranquilla (Colombia).
- Darst, C.R. and D.C. Cannatella. 2004. Novel relationships among hyloid frogs inferred from 12S and 16S mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* 31:462–475.
- Davidson, E.H. and B.R. Hough. 1969. Synchronous oogenesis in *Engystomops pustulosus*, a neotropical anuran suitable for laboratory studies: localization in the embryo of RNA synthesized at the lampbrush stage. *Journal of Experimental Zoology* 172:25–48.
- De la Riva, I.J. 1993. Ecología de una comunidad neotropical de anfibios durante la estación lluviosa. Doctor en Ciencias Biológicas Dissertation, Universidad Complutense de Madrid, Madrid.
- . 1997a. La fauna de anfibios del Parque Nacional de Coiba (Panamá): composición y biogeografía, p. 419–432 + color plate, p. 532. In S. Castroviejo and M. Velayos (eds.), *Flora y Fauna del Parque Nacional de Coiba (Panamá)*. *Inventario Preliminar*. Agencia Española de Cooperación Internacional, Madrid.
- . 1997b. Los anfibios, p. 85–88. In M. Velayos, C. Monge, F. Posse, and S. Castroviejo (eds.), *Guía de Campo del Parque Nacional de Coiba (Panamá)*. Agencia Española de Coiba (Panamá) Cooperación Internacional, Madrid.
- de Sá, R.O., W.R. Heyer, and A. Camargo. 2006 (2005). A phylogenetic analysis of *Vanzolinius* Heyer, 1974 (Amphibia, Anura, Leptodactylidae): taxonomic and life history implications. *Arquivos do Museu Nacional, Rio de Janeiro* 63:707–726.
- Dent, J.N. 1956. Observations on the life history and development of *Leptodactylus albilabris*. *Copeia* 1956:207–210.
- Dieguez, M., I. Domínguez, G. Ortega, A. Veces, Y.

- Araúz, D. Luque, A. Somoza, I. Tejada, M. Gallardo, and E. Nuñez. 2006. Componente de Calidad de Agua, Región Oriental de la Cuenca del Canal. Convenio de Cooperación ANAM-ACP, Monitoreo de la Cuenca Hidrográfica de Canal de Panamá, Panamá Ciudad.
- Dixon, J.R., J.A. Wiest, Jr., and J.M. Cei. 1993. Revision of the neotropical snake genus *Chironius* Fitzinger (Serpentes, Colubridae). Museo Regionale di Scienze Naturali, Torino, Monografie (13):1–279.
- Donnelly, M.A. 1994. Amphibian diversity and natural history, p. 199–209, 380–381. In L.A. McDade, K.S. Bawa, H.A. Hespenheide, and G.S. Hartshorn (eds.), *La Selva. Ecology and Natural History of a Neotropical Rain Forest*. The University of Chicago Press, Chicago.
- Donnelly, M.A. and C. Guyer. 1994. Patterns of reproduction and habitat use in an assemblage of neotropical hylid frogs. *Oecologia* 98:291–302.
- Downie, J.R. 1984. How *Leptodactylus fuscus* tadpoles make foam, and why. *Copeia* 1984:778–780.
- , R.H.L. Disney, L. Collins, and E.G. Hancock. 1995. A new species of *Megaselia* (Diptera, Phoridae) whose larvae prey upon the eggs of *Leptodactylus fuscus* (Anura, Leptodactylidae). *Journal of Natural History* 29:993–1003.
- and J. Smith. 2003. Survival of larval *Leptodactylus fuscus* (Anura: Leptodactylidae) out of water: developmental differences and interspecific comparisons. *Journal of Herpetology* 37:107–115.
- Duellman, W.E. 1966. The Central American herpetofauna: an ecological perspective. *Copeia* 1966:700–719.
- . 1967a. Social organization in the mating calls of some neotropical anurans. *The American Midland Naturalist* 77:156–163.
- . 1967b. Courtship isolating mechanisms in Costa Rican hylid frogs. *Herpetologica* 23:169–183.
- and L. Trueb. 1966. Neotropical hylid frogs, genus *Smilisca*. University of Kansas Publications, Museum of Natural History 17:281–375 + 12 plates.
- and –. 1986. *Biology of Amphibians*. McGraw-Hill Book Company, New York and other cities.
- Dunn, E.R. 1931a. The amphibians of Barro Colorado Island. *Occasional Papers of the Boston Society of Natural History* 5:403–421.
- . 1931b. Preliminary list of the reptiles and amphibians of the Canal Zone and the provinces of Panama and Colon, R.P. Barro Colorado Biological Station 7th Annual Report:15–18.
- . 1933a. A new *Hyla* from the Panama Canal Zone. *Occasional Papers of the Boston Society of Natural History* 8:61–64.
- . 1933b. Amphibians and reptiles from El Valle de Anton, Panama. *Occasional Papers of the Boston Society of Natural History* 8:65–79.
- . 1940. New and noteworthy herpetological material from Panama. *Proceedings of the Academy of Natural Sciences of Philadelphia* 92:105–122 + 1 plate.
- . 1954. The coral snake "mimic" problem in Panamá. *Evolution* 8:97–102.
- Dutta, S.K., K. Vasudevan, M.S. Chaitra, K. Shanker, and R.K. Aggarwal. 2004. Jurassic frogs and the evolution of amphibian endemism in the Western Ghats. *Current Science* 86:211–216.
- Echternacht, A.C. 1977. *How Reptiles and Amphibians Live*. Elsevier Phaidon, Oxford.
- Eckerlin, R. 1971. *Herpetological Research* [Abstract]. Connecticut Herpetological Society Bulletin (2):10.
- Erspamer, G.F. and J.M. Cei. 1970. Biogenic amines and active polypeptides in the skin of *Leptodactylus vilarsi* Melin. *Biochemical Pharmacology* 19:321–325.
- Erspamer, V. 1971. Biogenic amines and active polypeptides of the amphibian skin. *Annual Review of Pharmacology* 11:327–350.
- , J.M. Cei, and M. Roseghini. 1963. Occurrence of candicine (p-hydroxyphenylethyltrimethylammonium) in extracts of the skin of *Leptodactylus pentadactylus*. *Life Sciences* 11:825–827.
- and G.F. Erspamer. 1965. Biogenic amines and active polypeptides in the amphibian skin. *Rivista di Biologia (Perugia)* 58:259–270.
- , –, and J.M. Cei. 1986. Active peptides in the skins of two hundred and thirty American amphibian species. *Comparative Biochemistry and Physiology* 85C:125–137.
- , M. Roseghini, and J.M. Cei. 1964. Indole-, imidazole-, and phenyl-alkylamines in the skin of thirteen *Leptodactylus* species. *Biochemical Pharmacology* 13:1083–1093.
- , T. Vitali, M. Roseghini, and J.M. Cei. 1964. The identification of new histamine derivatives in the skin of *Leptodactylus*. *Archives of Biochemistry and Biophysics* 105:620–629.
- , –, –, and –. 1967. 5-methoxy- and 5-hydroxyindoles in the skin of *Bufo alvarius*. *Biochemical Pharmacology* 16:1149–1164.
- Fabrezi, M. and R. Vera. 1997. Caracterización morfológica de larvas de anuros del noroeste Argentino. *Cuadernos de Herpetología* 11:37–49.
- Flier, J., M.W. Edwards, J.W. Daly, and C.W. Myers. 1980. Widespread occurrence in frogs and toads of skin compounds interacting with the Ouabain site of Na<sup>+</sup>, K<sup>+</sup>-ATPase. *Science* 208:503–505.
- Fouquette, M.J., Jr. 1960. Call structure in frogs of the family Leptodactylidae. *The Texas Journal of Science* 12:201–215.
- Fox, H. 1984. *Amphibian Morphogenesis*. Humana Press, Clifton, New Jersey.
- Franzen, M. 1988. Beobachtungen an einigen Froschlurchen aus dem Santa Rosa-Nationalpark, Costa Rica. *Herpetofauna* 10:25–28.
- Gaige, H.T., N. Hartweg, and L.C. Stuart. 1937. Notes on a collection of amphibians and reptiles from eastern Nicaragua. *Occasional Papers of the Museum of Zoology, University of Michigan* (357):1–18.
- Gallardo, J.M. 1958. Observaciones biológicas sobre *Leptodactylus prognathus* Boulenger. *Ciencia e Investigación* 14:460–465.

- Gans, C. 1958. Herpetofauna of Turrialba, Costa Rica (compiled from Taylor & MCZ records). Instituto Interamericano de Ciencias Agrícolas, Turrialba, Costa Rica.
- Gibson, R.C. and K.R. Buley. 2004. Maternal care and obligatory oophagy in *Leptodactylus fallax*: a new reproductive mode in frogs. *Copeia* 2004: 128–135.
- Goin, C.J. 1959. Notes on the maxillary dentition of some frogs of the genera *Eleutherodactylus* and *Leptodactylus*. *Herpetologica* 15:134–136.
- Grant, T., D.R. Frost, J.P. Caldwell, R. Gagliardo, C.F.B. Haddad, P.J.R. Kok, D.B. Means, B.P. Noonan, W.E. Schargel, and W.C. Wheeler. 2006. Phylogenetic systematics of dart-poison frogs and their relatives (Amphibia: Athesphatanura: Dendrobatidae). *Bulletin of the American Museum of Natural History* (299):1–262.
- Gray, L.A. and A.S. Rand. 1997. A daybreak chorus in the frog, *Agalychnis callidryas*. *Journal of Herpetology* 31:440–441.
- Graybeal, A. 1997. Phylogenetic relationships of bufonid frogs and tests of alternate macroevolutionary hypotheses characterizing their radiation. *Zoological Journal of the Linnean Society* 119: 297–338.
- Green, A.J. 1990. Determinants of chorus participation and the effects of size, weight and competition on advertisement calling in the Tungara Frog, *Physalaemus pustulosus* (Leptodactylidae). *Animal Behaviour* 39:620–638.
- Green, T.M. 1999. A Lexicographic Study of Ulwa. Doctor of Philosophy Dissertation, Massachusetts Institute of Technology, Boston.
- Greene, H.W. 1988. Species richness in tropical predators. In F. Almeda, and C.M. Pringle (eds.), *Tropical Rainforests: Diversity and Conservation*. California Academy of Sciences Memoir (12): 259–280.
- . 1997. *Snakes: The Evolution of Mystery in Nature*. University of California Press, Berkeley.
- Gregory, P.T. 1983. Habitat structure affects diel activity pattern in the neotropical frog *Leptodactylus melanonotus*. *Journal of Herpetology* 17:179–181.
- Günther, A.C.L.G. 1900. Batrachia Salientia, p. 197–220. In F.D. Godman (ed.), *Biologia Centrali-Americana; or Contributions to the Knowledge of the Fauna and Flora of Mexico and Central America*. Zoology. Reptilia and Batrachia. Part 165. R.H. Porter, London.
- . 1902. Geographical distribution of the reptiles and batrachians represented in Mexico and Central America, p. x–xvii. In F.D. Godman (ed.), *Biologia Centrali-Americana; or Contributions to the Knowledge of the Fauna and Flora of Mexico and Central America*. Zoology. Reptilia and Batrachia, Part 165. R.H. Porter, London.
- Gunzburger, M.S. and J. Travis. 2005. Critical literature review of the evidence for unpalatability of amphibian eggs and larvae. *Journal of Herpetology* 39:547–571.
- Guyer, C. and M.A. Donnelly. 2004 (2005). Amphibians and Reptiles of La Selva, Costa Rica, and the Caribbean Slope: A Comprehensive Guide. University of California Press, Berkeley.
- Hardouin, J. 1997. Survey of the literature. Bureau for Exchange and Distribution of Information on Mini-Livestock 6:21–36.
- Hartdegen, R.W., M.J. Russell, and R. Buice. 1999. An enteric parasite survey of neotropical herpetofauna. *Herpetological Review* 30:26–28.
- Hawley, T.J. 2008. Common frogs of the Osa Peninsula, Costa Rica. *Rapid Color Guide* (246):1–2.
- Hayek, L.-A.C. and W.R. Heyer. 2005. Determining sexual dimorphism in frog measurement data: integration of statistical significance, measurement error, effect size and biological significance. *Anais da Academia Brasileira de Ciências* 77:45–76.
- Hayes, M.P., J.A. Pounds, and W.W. Timmerman. 1989. An annotated list and guide to the amphibians and reptiles of Monteverde Costa Rica. Society for the Study of Amphibians and Reptiles, *Herpetological Circular* (17):ii + 67 p.
- Heatwole, H.F. and O.J. Sexton. 1966. Herpetofaunal comparisons between two climatic zones in Panama. *The American Midland Naturalist* 75:45–60.
- Hedges, S.B. and M.P. Heinicke. 2007. Molecular phylogeny and biogeography of West Indian frogs of the genus *Leptodactylus* (Anura, Leptodactylidae). *Molecular Phylogenetics and Evolution* 44: 308–314.
- Hedges, S.B., W.E. Duellman, and M.P. Heinicke. 2008. New World direct-developing frogs (Anura: Terrarana): molecular phylogeny, classification, biogeography, and conservation. *Zootaxa* (1737): 1–182.
- Heinicke, M.P., W.E. Duellman, and S.B. Hedges. 2007. Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences, USA* 104:10092–10097 + supplementary materials.
- Henderson, C.L. 2002. *Field Guide to the Wildlife of Costa Rica*. University of Texas Press, Austin.
- Heyer, W.R. 1967. A herpetofaunal study of an ecological transect through the Cordillera de Tilarán, Costa Rica. *Copeia* 1967:259–271.
- . 1969a. The adaptive ecology of the species groups of the genus *Leptodactylus* (Amphibia, Leptodactylidae). *Evolution* 23:421–428.
- . 1969b. Studies on the genus *Leptodactylus* (Amphibia, Leptodactylidae) III. A redefinition of the genus *Leptodactylus* and a description of a new genus of Leptodactylid frogs. *Contributions in Science, Los Angeles County Museum* (155):1–14.
- . 1970 (1968). Studies on the genus *Leptodactylus* (Amphibia: Leptodactylidae). II. Diagnosis and distribution of the *Leptodactylus* of Costa Rica. *Revista de Biología Tropical* 16:171–205.
- . 1979. Systematics of the *pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smithsonian Contributions to Zoology* (301):1–43.
- . 1995. South American rocky habitat *Leptodactylus* (Amphibia: Anura: Leptodactylidae) with descrip-



- tion of two new species. *Proceedings of the Biological Society of Washington* 108:695–716.
- . 1998. The relationships of *Leptodactylus diedrus* (Anura, Leptodactylidae). *Alytes* 16:1–24.
  - . 2005. Variation and taxonomic clarification of the large species of the *Leptodactylus pentadactylus* species group (Amphibia: Leptodactylidae) from Middle America, northern South America, and Amazonia. *Arquivos de Zoologia* 37:269–348.
  - and M.M. Heyer. 2006. *Leptodactylus knudseni*. *Catalogue of American Amphibians and Reptiles* (807):1–12.
  - and D.S. Liem. 1976. Analysis of the intergeneric relationships of the Australian frog family Myobatrachidae. *Smithsonian Contributions to Zoology* (233):iii + 29 p.
  - and L.R. Maxson. 1982. Neotropical frog biogeography: paradigms and problems. *American Zoologist* 22:397–410.
  - , R.W. McDiarmid, and D.L. Weigmann. 1975. Tadpoles, predation and pond habitats in the tropics. *Biotropica* 7:100–111.
  - and A.S. Rand. 1977. Foam nest construction in the leptodactylid frogs *Leptodactylus pentadactylus* and *Physalaemus pustulosus* (Amphibia, Anura, Leptodactylidae). *Journal of Herpetology* 11:225–228.
  - and N.J. Scott, Jr. 2006. The advertisement call of *Leptodactylus laticeps* (Amphibia, Anura, Leptodactylidae): predatory aural luring? *Herpetological Natural History* 9:189–194.
  - and A.S. Thompson. 2000. *Leptodactylus rugosus*. *Catalogue of American Amphibians and Reptiles* (708):1–5.
- Höbel, G. 2000. Reproductive ecology of *Hyla rosenbergi* in Costa Rica. *Herpetologica* 56:446–454.
- . 2004a. Fortpflanzungsstrategien der Froschlurche Costa Ricas. Teil 1. Die Aquarien- und Terrarienzeitschrift 57(7):38–42.
  - . 2004b. Fortpflanzungsstrategien der Froschlurche Costa Ricas. Schluss. Die Aquarien- und Terrarienzeitschrift 57(8):24–27.
  - . 2008. The amphibians and reptiles of the Golfo Dulce region. Los anfibios y reptiles de la region del Golfo Dulce. *Stapfia* 88:305–328.
- Hödl, W. 1988. *Physalaemus ephippifer* (Leptodactylidae): Schaumnestbildung. Begleitveröffentlichungen zu wissenschaftlichen Filmen Film C 1891 des Österreichisches Bundesinstitut für den Wissenschaftlichen Film (Wien) Nr. 38/39:29–35.
- . 1990a. Reproductive diversity in Amazonian lowland frogs. *Fortschritte der Zoologie* 38:41–60.
  - . 1990b. An analysis of foam nest construction in the neotropical frog *Physalaemus ephippifer* (Leptodactylidae). *Copeia* 1990:547–554.
  - . 1992. Reproductive behaviour in the neotropical foam-nesting frog *Pleurodema diplolistris* (Leptodactylidae). *Amphibia-Reptilia* 13:263–274.
  - . 1996. Die Reptilien- und Amphibienfauna Costa Ricas, p. 56–76. In P. Sehnaal and H. Zettel (eds.), *Esquinas-Nationalpark. Der Regenwald der Österreicher in Costa Rica*. Naturhistorisches Museum Wien, Wien.
- House, P., A. Padilla, O. Munguía, and C. Molinero. 2002. Diagnóstico Ambiental: Reserva del Hombre y la Biosfera del Río Plátano. MOPAWI, AFE-COHDEFOR, UNAH and TNC, Tegucigalpa.
- Ibáñez D., R. 2005. A note on amphibians and reptiles in the upper Río Chagres basin, Panama, p. 237–242. In R.S. Harmon (ed.), *The Río Chagres, Panama: A Multidisciplinary Profile of a Tropical Watershed*. Springer, Dordrecht.
- , F.A. Arosemena, F.A. Solís, and C.A. Jaramillo A. 1995 (1994). Anfíbios y reptiles de la Serranía Piedras-Pacora, Parque Nacional Chagres. *Scientia (Panamá)* 9:17–31.
  - , C.A. Jaramillo A., M. Arrunátegui, Q.D. Fuenmayor, and F.A. Solís. 1997 (1995). Inventario biológico del Canal de Panamá. *Estudio herpetológico*. *Scientia (Panamá) Número Especial* (2):111–159.
  - , A.S. Rand, and C.A. Jaramillo A. 1999a. Los Anfíbios del Monumento Natural Barro Colorado, Parque Nacional Soberanía y Áreas Adyacentes. The Amphibians of Barro Colorado Nature Monument, Soberanía National Park and Adjacent Areas. Editorial Mizrahi and Pujol, S.A., Panamá.
  - , M.J. Ryan, and C.A. Jaramillo A. 1999b. Vocalizaciones de Ranas y Sapos del Monumento Natural Barro Colorado, Parque Nacional Soberanía y Áreas Adyacentes. Vocalizations of Frogs and Toads from Barro Colorado Nature Monument, Soberanía National Park and Adjacent Areas. Fundación Natura, Circulo Herpetológico de Panamá, Smithsonian Tropical Research Institute, Costa Rica.
  - , F.A. Solís, C.A. Jaramillo A., and A.S. Rand. 2001. An overview of the herpetology of Panama, p. 159–170. In J.D. Johnson, R.G. Webb, and O.A. Flores-Villela (eds.), *Mesoamerican Herpetology: Systematics, Zoogeography, and Conservation*. Centennial Museum, The University of Texas at El Paso, Special Publication (1).
- Jaeger, R.G. 1978. Ecological niche dimensions and sensory functions in amphibians, p. 169–196. In M.A. Ali (ed.), *Sensory Ecology: Review and Perspectives*, Vol. 18. Plenum Press, New York.
- and J.P. Hailman. 1981. Activity of neotropical frogs in relation to ambient light. *Biotropica* 13:59–65.
- Jara, F.G. 2008a. Tadpole-odonate larvae interactions: influence of body size and diel rhythm. *Aquatic Ecology* 42:503–509.
- . 2008b. Differential vulnerability of *Physalaemus pustulosus* tadpole size classes to predation by the water spider *Thaumasia* sp. (Physauridae). *Amphibia-Reptilia* 29:432–437.
- Jaramillo A., C.A., R. Ibáñez D., and A.S. Rand. 1994. Anfíbios y reptiles de Panamá. *Introducción*. *Naturaleza Tropical* (8):1–11.
- Jaslow, A.P. 1985. Variation in secondary sexual characters in *Leptodactylus pentadactylus* (Anura: Leptodactylidae) [Abstract]. *American Zoologist* 25:130A.
- . 1987. Variation in secondary sexual characters in *Leptodactylus pentadactylus* Anura: Leptodactylidae) [Abstract]. Joint Annual Meeting, Herpetologists' League and Society for the Study of Amphi-

- bians and Reptiles, Veracruz, México. 9–15 August, 1987.
- Johanboeke, M.M. 1974. Collecting on a Costa Rican cacao farm. *Bulletin of the Philadelphia Herpetological Society* 22:27–32.
- . 1977 (1976). Night collecting in Costa Rica. *Bulletin of the Philadelphia Herpetological Society* 24: 25–36.
- Johnston, M.R.L. 1975. Distribution of *Pirhemocytos* Chatton & Blanc and other, possibly related, infections of poikilotherms. *Journal of Protozoology* 22:529–535.
- Jungfer, K.-H. 1988. Froschlurche von Fortuna, Panama III. Leptodactylidae. *Herpetofauna* 10:15–21.
- Kaufmann, J.H. 1962. Ecology and social behavior of the coati, *Nasua narica* on Barro Colorado Island Panama. University of California Publications in Zoology 60:iv + 95–222 p.
- Kime, N.M., W.R. Turner, and M.J. Ryan. 2000. The transmission of advertisement calls in Central American frogs. *Behavioral Ecology* 11:71–83.
- Kluge, A.G. 1981. The life history, social organization, and parental behavior of *Hyla rosenbergi* Boulenger, a nest-building gladiator frog. University of Michigan Museum of Zoology, Miscellaneous Publications (160):[iii] + 170 p.
- Köhler, G. 1998. Herpetologische Beobachtungen in Nicaragua. *Natur und Museum* 128:162–170.
- . 1999. The amphibians and reptiles of Nicaragua. A distributional checklist with keys. *Courier Forschungsinstitut Senckenberg* (213):[i] + 121 p.
- . 2001. Anfíbios y Reptiles de Nicaragua. Herpeton, Verlag Elke Köhler, Offenbach, Germany.
- , J.R. McCranie, and K.E. Nicholson. 2000. Eine herpetologische Expedition in den Patuca-Nationalpark, Honduras. *Natur und Museum* 130:421–425.
- and R. Seipp. 1998. Eine Expedition in den Randbereich des Biosphärenreservats Bosawas, Nicaragua. *Natur und Museum* 128:170–175.
- Kotiaho, J.S. 2001. Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biological Reviews* 76:365–376.
- Kourany, M., C.W. Myers, and C.R. Schneider. 1970. Panamanian amphibians and reptiles as carriers of *Salmonella*. *The American Journal of Tropical Medicine and Hygiene* 19:632–638.
- Kratzer, H., S. Godfrin-Marchand, H. Keller, and R. Bechter. 1990. Costa Rica, herpetologisch kleinoord tussen de Atlantische en stille oceaan. *Terra (Belgium)* 26:123–128.
- Krywicki, J. 2001. Sunlight in the rain forest. *Reptiles Magazine* 9:10–27.
- Kubicki, B. 2008. Amphibian diversity in Guayacán, Limón province, Costa Rica. *Brenesia* 69:35–42.
- Lamothe-Argumedo, R. and B. Jaimes Cruz. 1982. Trematoda. Parasitic stages, p. 73–84. In S.H. Hurlbert, and A. Villalobos-Figueroa (eds.), *Aquatic Biota of Mexico, Central America and the West Indies*. San Diego State University, San Diego.
- , L. García-Prieto, D. Osorio-Sarabia, and G. Pérez-Ponce de León. 1997. Catálogo de la Colección Nacional de Helmintos Instituto de Biología Universidad Nacional Autónoma de México, Mexico.
- Larson, P.M. and R.O. de Sá. 1998. Chondrocranial morphology of *Leptodactylus* larvae (Leptodactylidae: Leptodactylinae): its utility in phylogenetic reconstruction. *Journal of Morphology* 238:287–305.
- , —, and D. Arrieta. 2003. Chondrocranial, hyobranchial and internal oral morphology in larvae of the basal bufonid genus *Melanophryniscus* (Amphibia: Anura). *Acta Zoologica (Stockholm)* 84:145–154.
- Laurencio, D. 2009. Amphibians and reptiles from Reserva Natural Absoluta Cabo Blanco, province of Puntarenas, Costa Rica. *Check List* 5:446–459.
- Lebron, R., A.T. Batra, J. Bontempo, C. Buckley, M. Cron, L. Fenstermacher, C. Mahoney, L. Schmitt, and A.M. Bauer. 1995. *Leptodactylus albilabris* (Caribbean White-lipped Frog). Larval diet. *Herpetological Review* 26:31.
- Leenders, T.A.A.M. 2001. A Guide to Amphibians and Reptiles of Costa Rica. Distribuidores Zona Tropical, S.A., Miami.
- Leigh, E.G., Jr. 2002. A Magic Web: The Forest of Barro Colorado Island. Oxford University Press, Oxford.
- Leistikow, A. 2001. Phylogeny and biogeography of South American *Chirinocheta*, traditionally placed in the family "Philosciidae" (Crustacea: Isopoda: Oniscidea). *Organisms Diversity and Evolution* 1: 1–85.
- LeVering, K.R. 1999. Why Frogs Scream: An Investigation of the Function of Distress Calling in *Leptodactylus pentadactylus*. Ph.D. Dissertation, University of Texas at Austin.
- Lewis, T.R. 2001. The herpetofauna of La Suerte Biological Field Station, Cariari, Costa Rica; an updated field list with notes on species recorded in 1998. *Herpetological Bulletin* (76):10–20.
- Lieberman, S.S. 1986. Ecology of the leaf litter herpetofauna of a neotropical rain forest: La Selva, Costa Rica. *Acta Zoologica Mexicana (n.s.)* (15): 1–72.
- Liner, E.A. 1994. Bibliography and scientific name index to amphibians and reptiles published in the Caribbean Journal of Science Volumes 1–25, 1961–1989. *Smithsonian Herpetological Information Service* (99):1–30.
- . 1997. Bibliography and scientific name index to the amphibians and reptiles of the Florida Academy of Sciences, Volume 1–55, 1937–1992, The Florida Field Naturalist, Volume 1–20, 1973–1992, and The Florida Naturalist, Volume 1–65, 1926–1992. *Smithsonian Herpetological Information Service* (113):1–39.
- . 1998. Bibliography and scientific name index to amphibians [sic] and reptiles in the Proceedings and Transactions of the Texas Academy of Science, Volume 1–30 (1892–1948), Special Publications of the Texas Academy of Science, 2 Editions (1936–1938), and the Texas Journal of Science, Volumes 1–45 (1949–1993). *Smithsonian*

- Herpetological Information Service (119):1–44.
- . 2009. Herpetological bibliography & scientific name index to the Bulletin of the Southern California Academy of Sciences, volumes 1–90, 1901–1991 & the Memoirs 1–10, 1938–1986. Smithsonian Herpetological Information Service (139):1–22.
- and C. Gans. 2004. Annotated bibliography of herpetological related articles in the National Geographic Magazine, volumes 1–194, 1890–1998. Smithsonian Herpetological Information Service (133):1–42.
- Lips, K.R. and J.M. Savage. 1996. Key to the known tadpoles (Amphibia: Anura) of Costa Rica. Studies on Neotropical Fauna and Environment 31: 17–26.
- , F. Brem, R. Brenes, J.D. Reeve, R.A. Alford, J. Voyles, C. Carey, L. Livo, A.P. Pessier, and J.P. Collins. 2006. Emerging infectious disease and the loss of biodiversity in a neotropical amphibian community. Proceedings of the National Academy of Sciences, USA 103:3165–3170 + 3 supporting Pages.
- , J.D. Reeve, and L.R. Witters. 2003. Ecological traits predicting amphibian population declines in Central America. Conservation Biology 17:1078–1088.
- Lourenço, L.B., M. Bacci-Júnior, V.G. Martins, S.M. Recco-Pimentel, and C.F.B. Haddad. 2008. Molecular phylogeny and karyotype differentiation in *Paratelmatobius* and *Scythrophrys* (Anura, Leptodactylidae). Genetica 132:255–266.
- Lutz, B. 1947. Trends towards non-aquatic and direct development in frogs. Copeia 1947:242–252.
- Lynch, J.D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactylid frogs. University of Kansas Museum of Natural History, Miscellaneous Publication (53):1–238.
- and C.M. Fugler. 1965. A survey of the frogs of Honduras. Journal of the Ohio Herpetological Society 5:5–18.
- Magnhagen, C. 1991. Predation risk as a cost of reproduction. Trends in Ecology and Evolution 6: 183–185.
- Malkin, B. 1956. Sumu ethnozoology: herpetological knowledge. Davidson Journal of Anthropology 2: 165–180.
- Malmström, R. 1993. Nationalparken Corcovado - ett guldställe för herpetologer. Snoken 23:14–21.
- Manzanilla Puppo, J., E. La Marca, and L. De Sousa. 2005. Ophiophagy and egg-eating in *Mannophryne* cf. *trinitatis* (Garman, 1888). Herpetozoa 18:69–71.
- Martínez Cortés, V. and A. Rodríguez. 2005. Datos preliminares sobre los anfibios y reptiles de Bahía Honda e Isla Canales de Tierra (Veraguas, Panamá). Preliminary data on amphibians and reptiles in Bahía Honda and Canales de Tierra Island (Veraguas, Panama), p. 571–626. In S. Castroviejo, and A. Ibáñez (eds.), Estudios sobre la Biodiversidad de la Región de Bahía Honda (Veraguas, Panamá). Studies on the Biodiversity of the Bahía Honda Region (Veraguas, Panama). Consejo Superior de Investigaciones Científicas, Instituto de España, Real Academia de Ciencias Exactas, Físicas y Naturales, Madrid.
- Marx, W.G. and G.R. Heath. 1992. Diccionario Miskito-Español, Español-Miskito. The Moravian Church in America, Bethlehem, Pennsylvania, Winston-Salem, North Carolina.
- Maxson, L.R. and W.R. Heyer. 1982. Leptodactylid frogs and the Brazilian Shield: an old and continuing adaptive relationship. Biotropica 14:10–15.
- and –. 1988. Molecular systematics of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). Fieldiana, Zoology, New Series (41):iii + 13 p.
- McCrane, J.R. 2006. Specimen locality data and museum numbers/Ubicación y números de museo de los especímenes, información complementaria for/a la "Guía de Campo de los Anfibios de Honduras" by/por James R. McCrane y Franklin E. Castañeda. Smithsonian Herpetological Information Service (137):1–39.
- . 2007. Distribution of the amphibians of Honduras by departments. Herpetological Review 38:35–39.
- and F.E. Castañeda. 2007a. Guía de Campo de los Anfibios de Honduras. Bibliomania!, Salt Lake City.
- and –. 2007b. Lista de anfibios de Honduras, p. 120–126. In H. Portillo, Recopilación de la Información sobre la Biodiversidad de Honduras. Instituto Nacional de Biodiversidad and Dirección General de Biodiversidad, Tegucigalpa.
- , –, and K.E. Nicholson. 2002. Preliminary results of herpetofaunal survey work in the Rus Rus Region, Honduras: a proposed biological reserve. Herpetological Bulletin (81):22–29.
- , J.H. Townsend, and L.D. Wilson. 2006. The Amphibians and Reptiles of the Honduran Mosquitia. Krieger Publishing Company, Malabar, Florida.
- and L.D. Wilson. 2002. The amphibians of Honduras. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology (19):x + 625 p. + 20 color plates.
- McDiarmid, R.W. and R. Altig. 1999a. Research: materials and techniques, p. 7–23. In R.W. McDiarmid, and R. Altig (eds.), Tadpoles: The Biology of Anuran Larvae. The University of Chicago Press, Chicago.
- and J.M. Savage. 2005. The herpetofauna of the Rincón area, Península de Osa, Costa Rica, a Central American lowland evergreen forest site, p. 366–427. In M.A. Donnelly, B.I. Crother, C. Guyer, M.H. Wake, and M.E. White (eds.), Ecology and Evolution in the Tropics. A Herpetological Perspective. The University of Chicago Press, Chicago.
- Mendez, E. 1987. Elementos de la Fauna Panameña. Imprenta Universitaria, Panama City.
- Mertens, R. 1960. The World of Amphibians and Reptiles. McGraw-Hill Book Company, Inc., New York.
- Metcalf, M.M. 1923. The opalinid ciliate infusorians. United States National Museum Bulletin (120):vii + 484 p.
- Meyer, J.R. 1969. A Biogeographic Study of the Am-



- phibians and Reptiles of Honduras. Doctor of Philosophy Dissertation, University of Southern California, Los Angeles.
- and L.D. Wilson. 1971. A distributional checklist of the amphibians of Honduras. Natural History Museum of Los Angeles County, Contributions in Science (218):1–47.
- Minton, S.A. and H.M. Smith. 1960. A new subspecies of *Coniophanes fissidens* and notes on Central American amphibians and reptiles. *Herpetologica* 16:103–111.
- Miranda, N.E.O. and A. Ferreira. 2008. Morfologia bucal interna dos girinos de *Leptodactylus labyrinthicus* Spix, 1824 (Amphibia: Anura: Leptodactylidae). *Biota Neotropica* 8:225–230.
- Miyamoto, M.M. 1981. Congruence among character sets in phylogenetic studies of the frog genus *Leptodactylus*. *Systematic Zoology* 30:281–290.
- Morescalchi, A. 1973. Amphibia, p. 233–348. In A.B. Chiarelli and E. Capanna (eds.), *Cytotaxonomy and Vertebrate Evolution*. Academic Press, London.
- and G. Gargiulo. 1968. Su alcune relazioni carilogiche del genere *Bufo* (Amphibia Salientia). *Rendiconti dell'Accademia di Scienze Fisiche e Matematiche della Società Nazionale di Scienze, Lettere ed Arti in Napoli, Serie* 35:117–120.
- Mudde, P. and M. van Dijk. 1983. *Herpetologische waarnemingen in Costa Rica (II): Fluitkikkers (Leptodactylidae)*. *Lacerta* 42:28–31.
- and –. 1985. *Herpetologische waarnemingen in Costa Rica* 14. *Opmerkingen voor de terrariumpraktijk, rektifikaties en literatuur*. *Lacerta* 43:197–201.
- Muedeking, M.H. and W.R. Heyer. 1976. Descriptions of eggs and reproductive patterns of *Leptodactylus pentadactylus* (Amphibia: Leptodactylidae). *Herpetologica* 32:137–139.
- Myers, C.W. and A.S. Rand. 1969. Checklist of amphibians and reptiles of Barro Colorado Island, Panama, with comments on faunal change and sampling. *Smithsonian Contributions to Zoology* (10):1–11.
- Nemuras, K.T. 1968. Notes on the Herpetology of Panama: Part 5. *Bulletin of the Maryland Herpetological Society* 4:8–19.
- . 1976. Flamboyant frogs of Panama. *Pacific Discovery (California Academy of Science)* 29:10–14.
- Nicholson, K.E., J.R. McCranie, and G. Köhler. 2000. Herpetofaunal expedition to Parque Nacional Patuca: a newly established park in Honduras. *Herpetological Bulletin* 2000:26–31.
- Noble, G.K. 1918. The amphibians collected by the American Museum Expedition to Nicaragua in 1916. *Bulletin of the American Museum of Natural History* 38:311–347 + plates 14–19.
- . 1927. The value of life history data in the study of the evolution of the Amphibia. *Annals of the New York Academy of Sciences* 30:31–128 + plate IX.
- Norman, D. 1998. *Common Amphibians of Costa Rica*. Anfíbios Comunes de Costa Rica. Privately printed, Heredia, Costa Rica.
- Palavecino, P.M. 1997. La musculatura mandibular e hioidea de la larva de *Leptodactylus chaquensis* (Anura: Leptodactylidae). *Cuadernos de Herpetología* 11:1–6.
- Palmer, W. 1992. Herpetofauna of Costa Rica. *Reptile and Amphibian Magazine* 1992:30–41.
- Park, O. 1938. Studies in nocturnal ecology, VII. Preliminary observations on Panama rain forest animals. *Ecology* 19:208–223.
- , A. Barden, and E. Williams. 1940. Studies in nocturnal ecology. IX. Further analysis of activity of Panama rain forest animals. *Ecology* 21:122–134.
- Petranka, J.W., M.E. Hopey, B.T. Jennings, S.D. Baird, and S.J. Boone. 1994. Breeding habitat segregation of wood frogs and American toads: the role of interspecific tadpole predation and adult choice. *Copeia* 1994:691–697.
- and C.A. Kennedy. 1999. Pond tadpoles with generalized morphology: is it time to reconsider their functional roles in aquatic communities? *Oecologia* 120:621–631.
- Polis, G.A. and C.A. Myers. 1985. A survey of intraspecific predation among reptiles and amphibians. *Journal of Herpetology* 19:99–107.
- Ponssa, M.L. 2005 (2004). Utilización espacial y temporal de una comunidad de anuros de Kent's Marsh (Gamboa, Panamá). *Revista Española de Herpetología* 18:5–18.
- and J.S. Barrionuevo. 2008. Foam-generating behaviour in tadpoles of *Leptodactylus latinasus* (Amphibia, Leptodactylidae): significance in systematics. *Zootaxa* (1884):51–59.
- Pough, F.H., J.B. Heiser, and W.N. McFarland. 1996. *Vertebrate Life*. Fourth edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey.
- Pounds, J.A. 2000. Amphibians and reptiles, p. 149–171. In N.M. Nadkarni and N.T. Wheelwright (eds.), *Monteverde: Ecology and Conservation of a Tropical Cloud Forest*. Oxford University Press, New York, Oxford.
- Pounds, J.A. and M.P. Fogden. 2000. Appendix 8. Amphibians and reptiles of Monteverde, p. 537–540. In N.M. Nadkarni and N.T. Wheelwright (eds.), *Monteverde: Ecology and Conservation of a Tropical Cloud Forest*. Oxford University Press, New York, Oxford.
- , J.M. Savage, and G.C. Gorman. 1997. Tests of null models for amphibian declines on a tropical mountain. *Conservation Biology* 11:1307–1322.
- Prado, C.P.A. and A. d'Heursel. 2006. The tadpole of *Leptodactylus elenae* (Anura: Leptodactylidae), with the description of the internal buccal anatomy. *South American Journal of Herpetology* 1: 79–86.
- , L.F. Toledo, J. Zina, and C.F.B. Haddad. 2005. Trophic eggs in the foam nests of *Leptodactylus labyrinthicus* (Anura, Leptodactylidae): an experimental approach. *Herpetological Journal* 15:279–284.
- , M. Uetanabaro, and C.F.B. Haddad. 2002. Description of a new reproductive mode in *Leptodactylus* (Anura, Leptodactylidae), with a review of

- the reproductive specialization toward terrestriality in the genus. *Copeia* 2002:1128–1133.
- Pröhl, H. 1997. Los Anfibios de Hitoy Cerere, Costa Rica. Talamanca, San José.
- Rabello, M.N. 1970. Chromosomal studies in Brazilian anurans. *Caryologia* 23:45–59.
- Rand, A.S. 1983. *Physalaemus pustulosus* (rana, sapito túngara, foam toad, mud-puddle frog), p. 412–415. In D.H. Janzen (ed.), *Costa Rican Natural History*. University of Chicago Press, Chicago.
- and C.W. Myers. 1990. The herpetofauna of Barro Colorado Island, Panama: an ecological summary, p. 386–409. In A.H. Gentry (ed.), *Four Neotropical Rainforests*. Yale University Press, New Haven.
- Renjifo, J.M. and M. Lundberg. 1999. Guía de Campo. Anfibios y Reptiles de Urrá. Editorial Colina, Medellín, Colombia.
- Roberts, W.E. 1997. *Leptodactylus pentadactylus* (Rana Ternero, Smoky Frog). Predation. *Herpetological Review* 28:84–85.
- Rodrigues, D.J., M. Menin, and A.P. Lima. 2007. Redescription of the tadpole of *Leptodactylus rhodomystax* (Anura: Leptodactylidae) with natural history notes. *Zootaxa* (1509):61–67.
- , M. Uetanabaro, and C.P.A. Prado. 2005 [2004]. Seasonal and ontogenetic variation in diet composition of *Leptodactylus podicipinus* (Anura, Leptodactylidae) in the southern Pantanal, Brazil. *Revista Española de Herpetología* 18:19–28.
- Rodríguez, A., V. Martínez-Cortés, and C. Garibaldi. 2005 [2004]. Inventario de anfibios en los bosques fragmentados de la Reserva Forestal El Montuoso, Provincia de Herrera, Panamá, p. 103–117 + color photos. In C. Garibaldi (ed.), *Diversidad Biológica y Servicios Ambientales de los Fragmentos de Bosque en la Reserva Forestal El Montuoso, Panamá*. Universidad de Panamá, Instituto de Ciencias Ambientales y Biodiversidad, Panamá.
- Romero-Martínez, H.J., C.C. Vidal-Pastrana, J.D. Lynch, and P.R. Dueñas. 2008. Estudio preliminar de la fauna anfibia en el Cerro Murrucucú, Parque Natural Nacional Paramillo y zona amortiguadora, Tierralta, Córdoba, Colombia. *Caldasia* 30:209–229.
- Rose, G.J., R. Zelick, and A.S. Rand. 1988. Auditory processing of temporal information in a neotropical frog is independent of signal intensity. *Ethology* 77:330–336.
- Roseghini, M., V. Erspamer, G.F. Erspamer, and J.M. Cei. 1986. Indole-, imidazole- and phenyl-alkylamines in the skin of one hundred and forty American amphibian species other than bufonids. *Comparative Biochemistry and Physiology* 85C: 139–147.
- Roth, L.M. and E.R. Willis. 1960. The biotic associations of cockroaches. *Smithsonian Miscellaneous Collections* 141:vi + 470 p. + Plates 1–36.
- Ruibal, R. and E. Thomas. 1988. The obligate carnivorous larvae of the frog, *Lepidobatrachus laevis* (Leptodactylidae). *Copeia* 1988:591–604.
- Ruiz Pérez, G.A. and F. Buitrago Vannini. 2003. Listado de los anfibios y reptiles de Nicaragua, p. 287–296. In G.A. Ruiz Pérez and F. Buitrago Vannini (eds.), *Guía Ilustrada de la Herpetofauna de Nicaragua*. ARAUCARIA-MARENA-AECI, Managua.
- Ruthven, A.G. 1922. The amphibians and reptiles of the Sierra Nevada de Santa Marta, Colombia. University of Michigan Museum of Zoology, Miscellaneous Publications (8):Frontispiece + 69 p. + 12 Plates + 1 Map.
- Ryan, M.J. 1985. The Túngara Frog. A Study in Sexual Selection and Communication. The University of Chicago Press, Chicago.
- and M.D. Tuttle. 1983. The ability of the frog-eating bat to discriminate among novel and potentially poisonous frog species using acoustic cues. *Animal Behaviour* 31:827–833.
- , –, and L.K. Taft. 1981. The costs and benefits of frog chorusing behavior. *Behavioral Ecology and Sociobiology* 8:273–278.
- Sasa, M. and A. Solórzano. 1995. The reptiles and amphibians of Santa Rosa National Park, Costa Rica, with comments about the herpetofauna of xerophytic areas. *Herpetological Natural History* 3:113–125.
- Savage, J.M. 1973a. A Preliminary Handlist of the Herpetofauna of Costa Rica. 1 ed. University of Southern California, Los Angeles.
- . 1973b. A Preliminary Handlist of the Herpetofauna of Costa Rica. 2 ed. University of Southern California, Los Angeles.
- . 1980a. A synopsis of the larvae of Costa Rican frogs and toads. *Bulletin of the Southern California Academy of Sciences* 79:45–54.
- . 1980b. A Preliminary Handlist of the Herpetofauna of Costa Rica. III Edition. Allan Hancock Foundation, University of Southern California, Los Angeles.
- . 1980c. A Handlist with Preliminary Keys to the Herpetofauna of Costa Rica. Allan Hancock Foundation, University of Southern California, Los Angeles.
- . 2002. The Amphibians and Reptiles of Costa Rica. A Herpetofauna between Two Continents, between Two Seas. The University of Chicago Press, Chicago.
- and F. Bolaños. 2009. A checklist of the amphibians and reptiles of Costa Rica: additions and nomenclatural revisions. *Zootaxa* (2005):1–23.
- and J. Villa. 1986. Introduction to the herpetofauna of Costa Rica. *Introducción a la herpetofauna de Costa Rica*. Society for the Study of Amphibians and Reptiles, Contributions to Herpetology (3):viii + 207 p.
- Schmidt, K.P. 1933. Amphibians and reptiles collected by the Smithsonian biological survey of the Panama Canal Zone. *Smithsonian Miscellaneous Collections* (89):1–20.
- Scott, N.J., Jr. 1983. *Leptodactylus pentadactylus* (Rana Ternero, Smoky Frog), p. 405–406. In D.H. Janzen (ed.), *Costa Rican Natural History*. University of Chicago Press, Chicago.

- and S. Limerick. 1983. Reptiles and amphibians, p. 351–367. *In* D.H. Janzen (ed.), Costa Rican Natural History. University of Chicago Press, Chicago.
- , J.M. Savage, and D.C. Robinson. 1983. Checklist of reptiles and amphibians, p. 367–374. *In* D.H. Janzen (ed.), Costa Rican Natural History. University of Chicago Press, Chicago.
- and A. Starrett. 1974. An unusual breeding aggregation of frogs, with notes on the ecology of *Agalychnis spurrelli* (Anura: Hylidae). *Bulletin of the Southern California Academy of Sciences* 73:86–94.
- Sexton, O.J., H.F. Heatwole, and D. Knight. 1964. Correlation of microdistribution of some Panamanian reptiles and amphibians with structural organization of the habitat. *Caribbean Journal of Science* 4:261–295.
- Sherratt, T.N. and I.F. Harvey. 1989. Predation by larvae of *Pantala flavescens* (Odonata) on tadpoles of *Phyllomedusa trinitatis* and *Physalaemus pustulosus*: the influence of absolute and relative density of prey on predator choice. *Oikos* 56:170–176.
- Silva, H.R. and J.R. Mendelson, III. 1999. A new organ and sternal morphology in toads (Anura: Bufonidae): descriptions, taxonomic distribution, and evolution. *Herpetologica* 55:114–126.
- Silva, M.B. and F.A. Juncá. 2006. Oophagy in tadpoles of *Leptodactylus troglodytes* (Amphibia, Anura, Leptodactylidae). *Sitientibus Série Ciências Biológicas* 6:89–91.
- Silva, W.R. and A.A. Giaretta. 2009. On the natural history of *Leptodactylus syphax* with comments on the evolution of reproductive features in the *L. pentadactylus* species group (Anura, Leptodactylidae). *Journal of Natural History* 43:191–203.
- , –, and K.G. Facure. 2005. On the natural history of the South American Pepper Frog, *Leptodactylus labyrinthicus* (Spix, 1824) (Anura: Leptodactylidae). *Journal of Natural History* 39:555–566.
- Skuk, G.O., M.G. Lima, F.A.C. Nascimento, and R.O. de Sá. 2007. Oviposição e descrição do girino de *Leptodactylus vastus* A. Lutz, 1930 (Anura: Leptodactylidae) [Abstract]. *Terceiro Congresso Brasileiro de Herpetologia*, Belém, Pará. 15 a 20 de Julho de 2007.
- Smith, H.M. 1987. Current nomenclature for the names and material cited in Günther's Reptilia and Batrachia volume of the *Biologia Centrali-Americana*, p. XXIII–LI. *In* K. Adler (ed.), Albert C.L.G. Günther, *Biologia Centrali-Americana*, Reptilia and Batrachia. Facsimile Reprints in Herpetology, Society for the Study of Amphibians and Reptiles, Ann Arbor, Michigan.
- Sousa, F. and F.A. Arosemena. 1991. Las ranas de Panamá. *Publicaciones Técnicas* (1):1–31.
- Starrett, P.H. 1968. The phylogenetic significance of the jaw musculature in anuran amphibians. Doctor of Philosophy Dissertation, University of Michigan, Ann Arbor.
- Straughan, I.R. and W.R. Heyer. 1976. A functional analysis of the mating calls of the neotropical frog genera of the *Leptodactylus* complex (Amphibia, Leptodactylidae). *Papéis Avulsos de Zoologia* 29:221–245.
- Summers, K. 2002. Relative abundance of leaf litter anurans in primary forest in the Nusagandi Biological Reserve, Republic of Panama. *Herpetological Natural History* 9:69–73.
- Suriano, D.M. 1970. Estudio sobre la fauna parasitaria de *Leptodactylus ocellatus* (L.) (Amphibia-Leptodactylidae) de la República Argentina. 1. Trematodes. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Ciencias Zoológicas* 10:215–239.
- Swanson, P.L. 1945. Herpetological notes from Panama. *Copeia* 1945:210–216.
- Tárano, Z. 1998. Cover and ambient light influence nesting preferences in the Túngara Frog *Physalaemus pustulosus*. *Copeia* 1998:250–251.
- Taylor, E.H. 1952. A review of the frogs and toads of Costa Rica. *University of Kansas Science Bulletin* 35, Part 1:577–942.
- Taylor, S.K., D.E. Green, K.M. Wright, and B.R. Whitaker. 2001. Bacterial diseases, p. 159–179. *In* K.M. Wright and B.R. Whitaker (eds.), *Amphibian Medicine and Captive Husbandry*. Krieger Publ., Malabar, Florida.
- Tejedo, M. 1991. Effect of predation by two species of sympatric tadpoles on embryo survival in Natterjack Toads (*Bufo calamita*). *Herpetologica* 47:322–327.
- Tejera Nuñez, V.H. and O.A. Dupuy Loo. 1994. Notas sobre anfibios de Panamá con referencia especial a la colección del Museo de Vertebrados de la Universidad de Panamá. *Scientia (Panamá)* 9:33–57.
- and –. 2003. Anfibios del Museo de Vertebrados de la Universidad de Panamá, Catálogo. Museo de Vertebrados de la Universidad de Panamá, Panamá.
- Thatcher, V.E. 1993. Trematódeos Neotropicais. *Instituto Nacional de Pesquisas da Amazonia*, Manaus.
- Toft, C.A. 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985:1–21.
- , A.S. Rand, and M. Clark. 1982. Population dynamics and seasonal recruitment in *Bufo typhonius* and *Colostethus nubicola* (Anura), p. 397–403. *In* E.G. Leigh, Jr., A.S. Rand, and D.M. Windsor (eds.), *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*. Smithsonian Institution Press, Washington, D.C.
- Toledo, L.F. and C.F.B. Haddad. 2009. Defensive vocalizations of neotropical anurans. *South American Journal of Herpetology* 4:25–42.
- , R.S. Ribeiro, and C.F.B. Haddad. 2007. Anurans as prey: an exploratory analysis and size relationships between predators and their prey. *Journal of Zoology, London* 271:170–177 + Appendix S1.
- , A.M. Tozetti, and J. Zina. 2005. *Leptodactylus labyrinthicus* (Pepper Frog): repertoire of defensive behaviour. *Herpetological Bulletin* (91):29–31.
- Tuttle, M.D. 1982. The amazing frog-eating bat. *National Geographic Magazine* 161:78–91.



- and M.J. Ryan. 1981. Bat predation and the evolution of frog vocalizations in the neotropics. *Science* 214:677–678.
- Valerio, C.E. 1971. Ability of some tropical tadpoles to survive without water. *Copeia* 1971:364–365.
- van Santen, M. 2006. Verdwenen juweeltjes, deel 1. *Lacerta* 64:117–130.
- Veloso M., A. 1977. Aggressive behavior and the generic relationships of *Caudiverbera caudiverbera* (Amphibia: Leptodactylidae). *Herpetologica* 33:434–442.
- Vera Candiotti, M.F. 2004. Morfología y alimentación de renacuajos de *Ceratophrys cranwelli* [Abstract]. V Congreso Argentino de Herpetología, San Juan, Argentina. 25–29 October 2004.
- . 2005. Morphology and feeding in tadpoles of *Ceratophrys cranwelli* (Anura: Leptodactylidae). *Acta Zoologica* (Stockholm) 86:1–11.
- . 2006. Ecomorphological guilds in anuran larvae: an application of geometric morphometric methods. *Herpetological Journal* 16:149–162.
- , F. Brusquetti, and F. Netto. 2007. Morphological characterization of *Leptodactylus elenae* tadpoles (Anura: Leptodactylidae: *L. fuscus* group), from central Paraguay. *Zootaxa* (1435):1–17.
- Vieira, W.L.S., G.G. Santana, and K.S. Vieira. 2007. Description of the tadpole of *Leptodactylus vastus* (Anura: Leptodactylidae). *Zootaxa* (1529):61–68.
- Villa, J. 1969 [1967]. Comportamiento defensivo de la "Rana Ternero," *Leptodactylus pentadactylus*. *Revista de Biología Tropical* 15:323–329.
- . 1971. Lista Tentativa de Vertebrados Inferiores de Nicaragua. Universidad Nacional Autónoma de Nicaragua, Managua.
- . 1972. Anfíbios de Nicaragua. Introducción a su Sistemática, Vida y Costumbres. Instituto Geográfico Nacional y Banco Central de Nicaragua, Managua.
- . 1983. Peces, Anfíbios y Reptiles Nicaraguenses: lista y Bibliografía. Nicaraguan Fishes, Amphibians and Reptiles: a Checklist and Bibliography. Escuela de Ecología y Recursos Naturales, Universidad Centroamericana, Managua.
- . 1984. Biology of a neotropical glass frog, *Centrolenella fleischmanni* (Boettger), with special reference to its frogfly associates. Milwaukee Public Museum, Contributions in Biology and Geology (55):1–60.
- , R.W. McDiarmid, and J.M. Gallardo. 1982. Arthropod predators of leptodactylid frog foam nests. *Brenesia* 19/20:577–589.
- , L.D. Wilson, and J.D. Johnson. 1988. Middle American Herpetology: A Bibliographic Checklist. University of Missouri Press, Columbia, Missouri.
- Vinton, K.W. 1938. A frog that eats bats and snakes. *National Geographic Magazine* 73:656–664.
- . 1951. Observations on the life history of *Leptodactylus pentadactylus*. *Herpetologica* 7:73–75.
- Vizotto, L.D. 1964. Amphibia, p. 387–417. In P.E. Vanzolini (ed.), *História Natural de Organismos Aquáticos do Brasil*. Fundação de Amparo à Pesquisa do Estado de São Paulo, São Paulo.
- . 1967. Desenvolvimento de anuros da região noro-  
cidental do Estado de São Paulo. Faculdade de Filosofia, Ciências e Letras de São José do Rio Preto, *Zoologia N.º Especial*:[iii] + 161 p.
- . 1984. *Ranicultura*. *Ciência e Cultura* 36:42–45.
- Wainwright, M. 2000. Costa Rica Field Guide. Amphibians. Double-sided plastic laminated sheet. Rainforest Publications, Costa Rica.
- Walley, H.D. 1997. Bibliography and scientific name index to herpetological publications by the University of Michigan Museum of Zoology 1913–1995. Smithsonian Herpetological Information Service (114):1–63.
- Wassersug, R.J. and W.R. Heyer. 1988. A survey of internal oral features of leptodactyloid larvae (Amphibia: Anura). Smithsonian Contributions to Zoology (457):iv + 99 p.
- Weaver, P.L. and G.P. Bauer. 2004. El Parque Nacional San Lorenzo: Resumen de Recursos Culturales y Naturales. Instituto Internacional de Dasonomía Tropical, San Juan, Puerto Rico.
- Weimer, R., F. Bolaños, W. Feichtinger, and M. Schmid. 1994. Die Amphibien von Costa Rica. Herpetologische Eindrücke einer Forschungsreise Teil V: Plethodontidae; zur ökologischen Situation der Froschlurche. *Sauria* 16:11–15.
- , W. Feichtinger, F. Bolaños, and M. Schmid. 1993a. Die Amphibien von Costa Rica. Herpetologische Eindrücke einer Forschungsreise Teil I: Einleitung, Hylidae (1) *Sauria* 15:3–8.
- , –, –, and –. 1993b. Die Amphibien von Costa Rica. Herpetologische Eindrücke einer Forschungsreise. Teil III: Leptodactylidae (1). *Sauria* 15:19–24.
- Wells, K.D. 1979. Reproductive behavior and male mating success in a neotropical toad, *Bufo typhoni*. *Biotropica* 11:301–307.
- . 2007. *The Ecology and Behavior of Amphibians*. The University of Chicago Press, Chicago.
- Wilson, L.D. 1983. Update on the list of amphibians and reptiles known from Honduras. *Herpetological Review* 14:125–126.
- and J.R. Meyer. 1972. Book review: Anfíbios de Nicaragua: Introducción a su Sistemática, Vida y Costumbres. By Jaime Villa. *Herpetological Review* 4:219.
- and J.R. McCranie. 1993. Preliminary key to the known tadpoles of anurans from Honduras. Royal Ontario Museum, Life Sciences Occasional Paper (40):1–12.
- and –. 1994. Second update on the list of amphibians and reptiles known from Honduras. *Herpetological Review* 25:146–150.
- and –. 1998. The biogeography of the herpetofauna of the subhumid forests of Middle America (Isthmus of Tehuantepec to northwestern Costa Rica). Royal Ontario Museum, Life Sciences Contributions (163):[i] + 50 p.
- and –. 2004 [2003]. The conservation status of the herpetofauna of Honduras. *Amphibian and Reptile Conservation* 3:6–33.
- , –, and M.R. Espinal. 2001. The ecogeography of the Honduran herpetofauna and the design of biotic reserves, p. 109–158. In J.D. Johnson, R.G.

- Webb, and O.A. Flores-Villela (eds.), *Mesoamerican Herpetology: Systematics, Zoogeography, and Conservation*. Centennial Museum, The University of Texas at El Paso, Special Publication (1).
- and J.H. Townsend. 2006. The herpetofauna of the rainforests of Honduras. *Caribbean Journal of Science* 42:88–113.
- Wollerman, L. and R.H. Wiley. 2002. Possibilities for error during communication by neotropical frogs in a complex acoustic environment. *Behavioral Ecology and Sociobiology* 52:465–473.
- Wunder, W. 1932. Nestbau und Brutpflege bei Amphibien, p. 180–220. *In* H. Winterstein (ed.), *Ergebnisse der Biologie*. Achter Band. Verlag von Julius Springer, Berlin.
- Yamaguti, S. 1971. Synopsis of Digenetic Trematodes of Vertebrates. Volume I. Keigaku Publishing Co., Tokyo.
- Young, B.E., G. Sedaghatkish, E. Roca, and Q.D. Fuenmayor. 1999. El Estatus de la Conservación de la Herpetofauna de Panamá. Resumen del Primer Taller Internacional sobre la Herpetofauna de Panamá. The Nature Conservancy and Asociación Nacional para la Conservación de la Naturaleza (ANCON), Arlington, Virginia.
- Zelick, R., G.J. Rose, and A.S. Rand. 1991. Differential response to frequency modulation rate and direction by the neotropical frog, *Physalaemus pustulosus*. *Animal Behaviour* 42:413–421.
- Zelmer, D. and D.R. Brooks. 2000. *Halipegus eschi* n. sp. (Digenea: Hemiuridae) in *Rana vaillanti* from Guanacaste Province, Costa Rica. *Journal of Parasitology* 86:1114–1117.
- Zetek, J. and A. Wetmore. 1951. Appendix 10. Report on the Canal Zone biological area. Smithsonian Institution, Washington.
- Zina, J. and C.F.B. Haddad. 2005. Reproductive activity and vocalizations of *Leptodactylus labyrinthicus* (Anura: Leptodactylidae) in southeastern Brazil. *Biota Neotropica* 5:1–11.

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